Impact of Human and Other Disturbance on Behaviour and Heart Rate of Incubating Adélie Penguins (*Pygoscelis adeliae*)

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APPENDIX: see Supplementary Volume and CD 2

Supplementary Volume – Contents

1 Introduction

> "Expeditionsreisen in die Antarktis zählen zu den letzten **Abenteuern** unserer Zeit. Wenn mächtige Eisberge lautlos vorbeiziehen, die riesenhafte Fluke eines Wals durch das Wasser bricht oder Sie an den Küsten mit zehntausenden **Pinguinen** anlanden, dann erwacht ein ursprünglicher Geist in Ihnen – der Entdeckergeist."[1] (www.abenteuer-antarktis.de; boldface added)
>
> "Travel in general has become relatively cheap and fast-growing, and **adventure** travel – which includes the **penguin** trail to Antarctica – is the fastest-growing sector of all. […] Everyone wants to visit **penguins**, seals and whales on their home ground." (STONEHOUSE 2000, p. 1; boldface added)
>
> "The spirit of **adventure**, under many guises, is what lures most people to Antarctica." (AINLEY 2002, p. 1; boldface added)

According to the quotes above, there are two main incentives for **human presence in Antarctica**, viz., 'adventure[2]' and wildlife, with the latter including – mostly quite at the top of the list – penguins. While one or both of these apply to the majority of tourists and scientists, economic benefits constitute a third reason, additionally or even predominantly relevant with respect to support personnel (scientific and 'touristic', resp.) nowadays, as well as to the sealers and whalers 'of old'. The interplay of these motivations represents a crucial determinant for individual human conduct towards Antarctic wildlife and thus penguins.

Antarctic penguins are susceptible to **human interference**. Predominantly water-based during the non-reproductive phase, they come ashore to breed in colonies – which serve as a 'natural' attractant to humans. Moreover, sites suitable for the establishment of penguin colonies are often equally suitable for the establishment of research stations, and penguin landing beaches will often be equally accessible to zodiacs[3] used in touristic or scientific (ad)ventures. For Antarctic penguins, successful reproduction is heavily dependent on 'resource management' and timing, as the birds do not feed while ashore; and climatic conditions do not permit much flexibility in the breeding 'schedule'. In the course of evolution, these prerequisites have led to a high degree of nest site tenacity during incubation, which might easily evoke the impression of the birds being 'unruffled' by close human approach.

Most of the **unequivocal disturbances** to penguins have been successfully addressed to date in a number of Antarctic legal documents, e.g., dogs (Annex II of the Madrid Protocol on Environmental Protection to the Antarctic Treaty, 1991), discharge of firearms, use of explosives, or driving of vehicles (Agreed Measures for the Conservation of Antarctic Flora and Fauna, 1964).

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[1] Quoted from the Hapag Lloyd online brochure, Oct. 2010; approximate translation: "Expedition cruises to the Antarctic are among the last adventures of our time. When mighty icebergs silently drift by, when the giant fluke of a whale cuts through the surface of the water, when you land on coasts populated by ten thousands of penguins – then you feel an original spirit awakening in you: the spirit of the discoverer." (Transl.: K.Schuster)

[2] which, for tourists at least, generally excludes physical discomfort

[3] Zodiacs (rubber boats) are used for short-distance transport, e.g. transfer of tourists from cruise ship to shore, and their invention constituted an important contributing factor to the increase in tourism (HEADLAND 1994).

The **extent of (acceptable) impact of human visitation** on Antarctic penguins, in contrast, has been controversially debated for a long time, particularly in the light of comparison of evils (the more you know about something, the more readily you will care for it vs. while getting to know it, you will – possibly quite inadvertently – tarnish or destroy some or all of it). Findings both for and against impact of a number of human activities on a number of penguin species have been provided by a number of authors using a number of parameters to measure this impact. In the meantime, Antarctic scientific activity as well as Antarctic tourism has increased substantially. The global economic crisis has brought some alleviation in terms of reduced numbers of people, but this would appear to be only a temporary respite for the penguins as the fascination of Antarctica continues unabated (e.g., Hapag Lloyd quote, advertising for the coming season).

Human presence in the Antarctic must therefore be considered a fact, and its numerical reduction in the foreseeable future seems highly unlikely. **Human conduct** thus becomes the only ‘adjusting screw’ available to reduce the potential for negatively impacting upon Antarctic wildlife. Conduct is mediated by motivation (s.a.), which, in turn, is influenced by knowledge/ awareness.

Changes in human impact through changes in awareness have been effected in other fields of science, e.g., published research from **Animal Welfare Science** has increased public concern about welfare problems with respect to laboratory, farm, and companion animals, and has led to improvements in a number of – though by no means all – areas. This discipline uses a combination of behavioural and physiological parameters to measure detrimental influence on the welfare of individuals and/or groups. Animal Welfare Science, however, has to date not greatly featured in the Antarctic.

Within the legal framework of the Antarctic Treaty System and the conceptual framework of Animal Welfare Science, **the thesis presented here** examines the impact of different types of human visitation on behaviour, posture, and heart rate of incubating Adélie penguins (*Pygoscelis adeliae*).

To do this, a total of **seven objectives** are addressed: The strength of impact is quantified in focal groups (behaviour, posture) and individual focal animals (behaviour, posture, heart rate). The extent of individuality of responses of focal animals is looked at to detect employment of different coping strategies and to thus determine whether ‘average responses’ represent an adequate measure of the impact of disturbance. Penguin responses to human visitation are compared to those observed during conspecific disturbance to ‘ground’ the extent of human impact to a natural stressor and to gain insight into the ‘relative importance’ the penguins might attribute to either disturbing agent. Impact of different visiting regimes is examined to identify key features alleviating/ enhancing impact. Ideally this will lead to the identification of indicative behaviours which would help even untrained observers to reliably gauge their impact on the penguins. Additionally, these might be employed to design robust threshold distances, adherence to which would markedly reduce signs of disturbance.

Within the context of all seven aims, **discriminatory capacities of different sampling and transcription methods** will be compared as to their sensitivity concerning detection of changes in behaviour, posture and/ or heart rate.

2 Theoretical Background

The study presented here constitutes an etho-physiological investigation of human impact on incubating Adélie penguins, based on fieldwork conducted in Antarctica. To serve as a comprehensive theoretical basis, the following chapter therefore draws upon rather diverse areas of research.

Overviews of **Antarctica** and the legal framework of the **Antarctic Treaty System** are followed by an outline on the different **human activities** and their potential **impact on Antarctic fauna**, with particular reference to tourism and scientific presence.

Subsequently, scientific fields relevant to the design of THIS STUDY are presented, viz., **animal welfare science** and **conservation behaviour**, and studies conducted on human disturbance are reviewed.

The section will conclude with the **aims** of this thesis and the **hypotheses** examined.

N.b.: To avoid misattributions, references to the study presented here will be set in SMALL CAPITALS (i.e., THIS STUDY/ THIS THESIS etc. refers to the study presented here).

2.1 Antarctica and the Antarctic Treaty System

2.1.1 Antarctica

> “Antarctica is the world’s largest and most pristine wilderness, covering an area of nearly 14 million square kilometres. Activities in the Antarctic are regulated by the Antarctic Treaty (1961) which applies to the area south of 60° south latitude, including all islands and ice shelves.”[1]

The Antarctic **coastline** measures 32,000 km in length. Together with the contiguous **Southern Ocean**, the Antarctic continent covers approximately 50 million square kilometres or 10 % of the world’s surface (HALL 1992). The **continent** of Antarctica is almost twice the size of Australia or Europe, three-quarters that of South America, and 37 or even 40 times that of Germany[2] . It exceeds the combined extent of China and India, or of the US and Mexico (BECK 1990a). The **ocean basin** surrounding the continent has a mean depth of 4,000 m. Figure 2-1 shows a map of Antarctica not found in the majority of atlases. With the continent placed in the centre of the map instead of being depicted as a ‘smudge’ on its uppermost edge, the size of Antarctica is brought into perspective.

The Antarctic continent is separated into the two geologically different provinces of East and West Antarctica, which together form a rough comma-shape (STONEHOUSE 2000; see fig. 2-2): **East Antarctica** is the ‘comma body’, while **West Antarctica** represents the ‘comma tail’ (also known as ‘Antarctica’s panhandle’), with the **Antarctic Peninsula** pointing towards South America. East Antarctica is a coherent land area, whereas West Antarctica actually comprises an archipelago of islands beneath the ice.[3] Ranging from Victoria Land (Ross Sea) to Coats Land (Weddell Sea), the tectonically active **Transantarctic Mountains** constitute the 5th longest mountain range in the world (3,500 km), and Mount Erebus (3,794 m) on Ross Island (to the left and at the mouth of McMurdo Sound; see fig. 3-19 in chapter 3.2 – Location) is the southernmost active volcano.[4]

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[1] quoted from http://cep.ats.aq/cep/apa/introduction/index.html

[2] Both figures are provided by German Umweltbundesamt.

[3] http://www.umweltbundesamt.de/antarktis/

[4] translated from http://www.umweltbundesamt.de/antarktis/

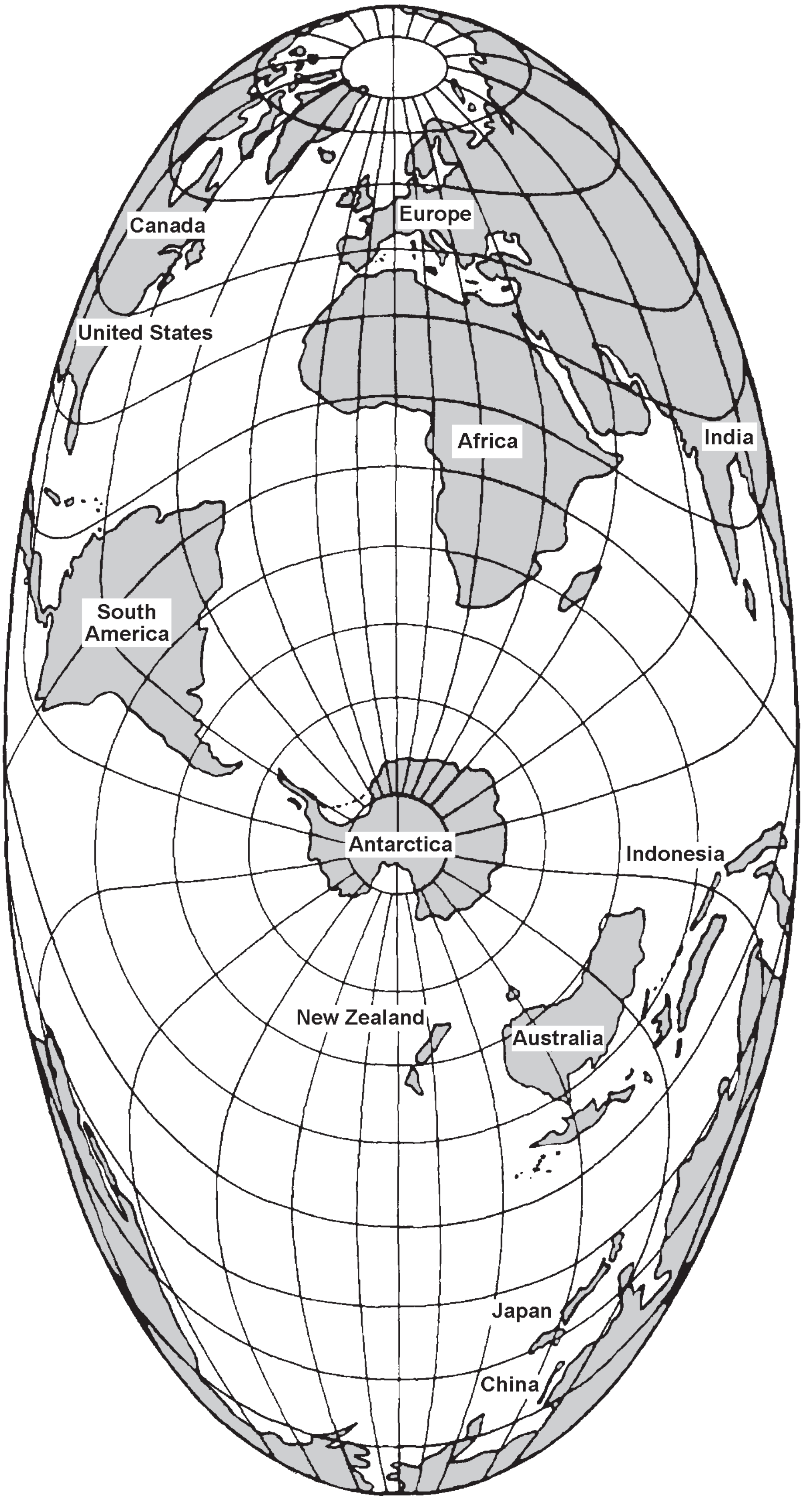

Figure 2-1: The World Viewed from Antarctica. Beck's focus provides an alternative perspective to that offered by most world maps. Redrawn from Beck (1990a).

Antarctica's **ice sheet** exhibits a mean thickness of 1.8 km, with the highest point of the ice sheet, Dome Argus in East Antarctica, rising to just above 4 km. The layer of ice covers 98 % of Antarctica's surface, including 96 % of its true shoreline. According to Stonehouse (2000, p. 10), "Antarctica carries approximately 30 million cubic kilometres of ice, about 90 % of all the ice currently in the world".

Several **boundaries** apply to Antarctica (see fig. 3-19 in chapter 3.2 – Location). The **Polar Circle** is a line drawn 23°27' or 2589 km distant from the South Geographical Pole (Stonehouse 2000). The **Antarctic Convergence** (or Antarctic Polar Front) is the oceanographic boundary of the Antarctic. It constitutes "the agreed-upon northern boundary of the Southern Ocean" (Ainley 2002, p. 26); and Joyner (1996) mentions that diplomats use it for setting the northernmost jurisdictional reach of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR 1980). Generally situated between 55°S and 60°S latitude, the Antarctic Convergence is the area in which the colder, denser surface water of the Southern Ocean meets the warmer, less dense surface water of the sub-Antarctic (temperate) zone (Ainley 2002). The **Antarctic Treaty Area** (see below) is, by agreement, defined as

> "the area south of 60°S Latitude, including all ice shelves, but nothing in the present Treaty shall prejudice or in any way affect the rights, or the exercise of the rights of any State under international law with regard to the high seas within that area." (Antarctic Treaty, Article VI)

Only just over 1 % of the land area within 60°S is ever free of snow and ice, and much of the area of snow-free ground on continental Antarctica is close to the coast. According to Walton (1987, p. 83), "[t]hese areas of rock and soil contain nearly all the biological diversity of Antarctica […]". Rather unfortunate for Antarctica's natural inhabitants, the same areas have turned out to be those most attractive to humans for a variety of activities (i.e., animal exploitation, the majority of scientific and tourism operations). In the words of Young (1990, p. 231):

> "People have similar requirements to penguins and skuas for ice-free terrain near open water."

2.1.2 The Antarctic Treaty System

Due to its evolutionary and plate-tectonical history, Antarctica lacks a native human population and thus 'natural owners'. In the course of discovering and exploring the continent, however, seven nations[5] staked their territorial **claims** on Antarctica (fig. 2-2), legalising these claims during the early- to mid-20th century. As Stonehouse (2000, p. 251) puts it:

> "These claims were valid in the sense that they were notified to the international community in the proper way, though three of them – Argentine, British and Chilean – overlapped seriously. Between them they account for some 85 % of the continent; leaving unclaimed only a virtually inaccessible sector of West Antarctica."

For the time being, territorial claims outlined in figure 2-2 have been 'put on ice' by common agreement, but they have not been dropped. The **Antarctic Treaty** entered into force in 1961, proclaiming that

> "[…] it is in the interest of all mankind that Antarctica shall continue for ever to be used exclusively for peaceful purposes and shall not become the scene or object of international discord." (Preamble)

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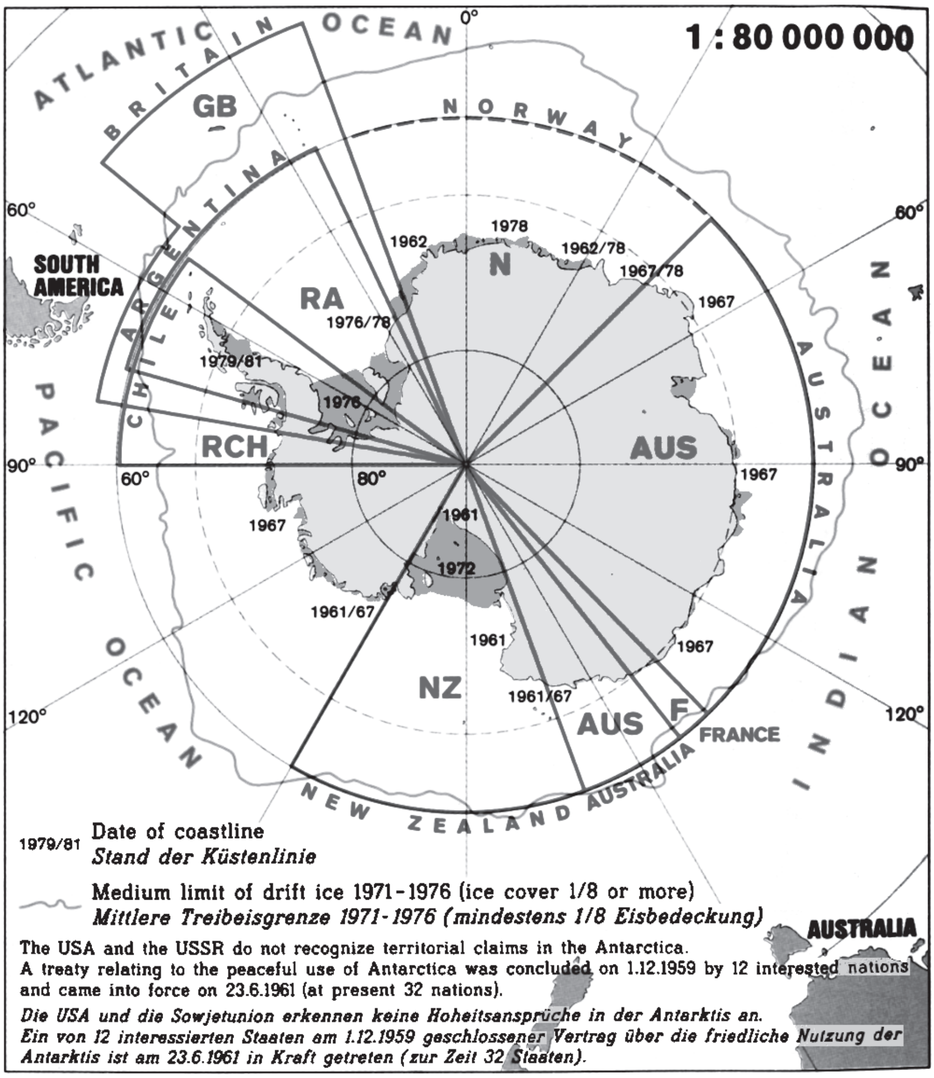
[5] claimant nations: Norway, Australia, France, New Zealand, Chile, the UK, and Argentina



1979/81 Date of coastline
Stand der Küstenlinie

Medium limit of drift ice 1971-1976 (ice cover 1/8 or more)
Mittlere Treibeisgrenze 1971-1976 (mindestens 1/8 Eisbedeckung)

The USA and the USSR do not recognize territorial claims in the Antarctica.
A treaty relating to the peaceful use of Antarctica was concluded on 1.12.1959 by 12 interested nations and came into force on 23.6.1961 (at present 32 nations).

*Die USA und die Sowjetunion erkennen keine Hoheitsansprüche in der Antarktis an.
Ein von 12 interessierten Staaten am 1.12.1959 geschlossener Vertrag über die friedliche Nutzung der Antarktis ist am 23.6.1961 in Kraft getreten (zur Zeit 32 Staaten).*

Figure 2-2: Antarctica. Territorial claims have merely been frozen for the time of the Antarctic Treaty. From AIS – Antarktische Informations- und & Schutzgemeinschaft (1986)

The twelve nations that originally drew up and signed the Antarctic Treaty[6] intended to secure cooperation between all nations with interests in Antarctica, while avoiding the question of ownership. Together with those nations that have since joined the Treaty[7] , they form the Consultative Parties to the Antarctic Treaty System, and have become the “de facto managers” (Stonehouse 2000) of Antarctica. The Antarctic Treaty came into being after the first **International Geophysical Year** (IGY, 1957/ 1958) during which these twelve nations (comprising scientists from 67 countries[8]) cooperated peacefully and effectively in scientific research. At the end of the IGY, however, research bases had come into existence, which might have easily been converted for military purposes after the end of the ‘one-year-truce’. It was thus as much for **political reasons** as for **scientific purposes** that a formal agreement between nations was sought, to ensure continuing cooperation and to thwart any dawning thoughts of warfare. The Antarctic Treaty was negotiated between June 1958 and May 1959, signed in Washington by representatives of the twelve IGY nations on 1 December 1959, and brought into force 23 June 1961. In addition to assuring the continuation of

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[6] Argentina, Australia, Belgium, Chile, France, Japan, New Zealand, Norway, ‘the Union of South Africa’, the [then] ‘Union of Soviet Socialist Republics’, the UK, and the USA

[7] By April 2010, there were 48 treaty member nations, 28 Consultative and 20 non-Consultative; consultative (decision-making) members include the seven nations that claim portions of Antarctica as national territory and 21 non-claimant nations (https://www.cia.gov./library/publications/the-world-factbook/geos/ay.html).

[8] figure provided at http://www.umweltbundesamt.de/antarktis/index.htm#tourismus

cooperative research and the protection of the Antarctic environment, the Treaty requires the setting aside of all claims to sovereignty, prohibits nuclear testing, allows for unilateral inspection, and demilitarises the entire treaty area (Zumberge 1987).

The treaty itself is a simple document (preamble, 14 articles). Based upon this document, however, a system of governance has been developed that has come to be called the **Antarctic Treaty System (ATS)**. According to the 9th edition of the Handbook of the Antarctic Treaty System (ed. Cohen 2002), it includes the Antarctic Treaty, the measures in effect under that treaty, its associated separate international instruments in force and the measures in effect under those instruments.

Both the German Democratic Republic (November 1974) and the Federal Republic of Germany (February 1979) signed the Antarctic Treaty as Acceding Parties[9], and subsequently became Consultative Parties[10] in reverse order (GDR: October 1987; FRG: March 1981). From the date of German unity (3 October 1990), the Federal Republic of Germany acts under the designation of '**Germany**' within the framework of the Antarctic system (Handbook of the Antarctic Treaty System 2002, pp. 12f.).

The Antarctic Treaty creates no **law** of its own. Instead, the Contracting[11] Parties to the Antarctic Treaty (ATCPs) appoint representatives to participate in the **Antarctic Treaty Consultative Meetings (ATCMs)**. On these meetings, 'measures[12]' and 'resolutions[13]' are agreed upon, which the delegates subsequently pass on to their respective governments for ratification[14]. Among those 'agreements' are (Bonner 1990; Cohen 2002)

- the 'Agreed Measures for the Conservation of Antarctic Flora and Fauna' (1964),
- the 'Convention for the Conservation of Antarctic Seals' (**CCAS**, 1972[15]),
- the 'Convention on the Conservation of Antarctic Marine Living Resources' (**CCAMLR**[16], 1980[17]),
- and the 'Protocol on Environmental Protection to the Antarctic Treaty[18]' (199l[19]), a.k.a. 'Madrid Environmental Protocol'.

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[9] Acceding Parties agree to be bound by the treaty and its measures, but are not active in research and have no rights of discussion or voting (Stonehouse 2000, p. 260). With respect to meetings, they are referred to as non-Consultative Parties.

[10] Consultative Parties qualify by pursuing scientific research in Antarctica, and have full rights to discussion and voting (Stonehouse 2000, p. 260).

[11] Contracting Parties are all those who have signed the Antarctic Treaty, be they Consultative or non-Consultative.

[12] Measures are mandatory, i.e. they have to be taken into each government's national legislation (Stonehouse 2000, p. 261).

[13] Resolutions are advisory, for governments to follow but not necessarily to cover by legislation (Stonehouse 2000, p. 261).

[14] e.g., AUG: Gesetz zur Ausführung des Umweltschutzprotokolls zum Antarktis-Vertrag = transfer of the 'Protocol on Environmental Protection to the Antarctic Treaty' into German legislation

[15] date of entry into force: 1978

[16] CCAMLR operates through a Commission known by the same acronym (Bonner 1990).

[17] date of entry into force: 1982

[18] In German: Umweltschutzprotokoll zum Antarktis-Vertrag (USP), or 'Madrid-Protokoll'; incorporated into German legislation since 1998 (AUG = Gesetz zur Ausführung des Umweltschutzprotokolls zum Antarktis-Vertrag).

[19] Agreed in 1991, it did not enter into force until 1998, and some of its Annexes took even longer than that.

As far as **science** is concerned, the non-governmental **Scientific Committee on Antarctic Research (SCAR)** constitutes the most important organisation. “Under the auspices of ICSU[20]” (Zumberge 1987, p. 4), SCAR was founded in Stockholm at the time of the International Geophysical Year (IGY) in 1957. It was originally named the Special Committee on Antarctic Research, but in 1960 SCAR substituted ‘special’ with ‘scientific’ and thus became the Scientific Committee on Antarctic Research. Zumberge (1987, p. 5; italics in quote) points out that, unlike the Consultative Parties, who receive their authority from the Antarctic Treaty,

> “the authority of SCAR is *not* based on the authority of the SCAR constitution, but rather on the experience and scientific reputations of the men and women who represent the international scientific community as SCAR Delegates or members of SCAR Working Groups. Collectively, these experts constitute the greatest concentration of talent engaged in Antarctic science and associated technology ever assembled”.

SCAR has become the principal advisory body to Contracting Parties to the Antarctic Treaty (ATCPs; Joyner 1996), lending its expertise to questions pertaining to, e.g., logistics, telecommunication, living resources of the Southern Ocean, effects of mineral resource exploration and exploitation[21], measures of Antarctic conservation, and the designation of protected areas (Zumberge 1987).

Beck (1988, quoted in Beck 1990a, p. 250) called Antarctica “**a continent surrounded by advice**”, referring to the 1980s, when in the context of debating the most appropriate management mechanism for scientific, environmental and resource issues, Antarctica was “deemed worthy of consideration” by the UN and a range of other international organisations, and a series of reports were published on that matter.

From the mid-1980s to mid-1990s, Antarctic conservation issues received much public attention and were broadly discussed in at least three special issues of journals covering very different areas of research (Environment International 1987, Applied Geography 1990, and Annals of Tourism Research 1994).

According to Joyner (1996, p. 183), the **Madrid Environmental Protocol** (= Protocol on Environmental Protection to the Antarctic Treaty; signed 1991, entered into forced 1998) signalled a “reversal in course” with respect to the ATCPs’ political and economic aspiration for the Antarctic:

> “Whereas in the late 1980s the policy direction of the [AT]CP group appeared headed towards possible exploration and potential exploitation of Antarctic minerals and hydrocarbons, by 1991 that course had been diverted towards a general commitment of legal obligation to conserve and protect comprehensively the continent and its circumpolar seas.”

2.1.3 General Information on Antarctic Protected Areas

> “Under the Antarctic Treaty System, the concept of setting aside areas for special protection was first introduced by the Agreed Measures for the Conservation of Antarctic Flora and Fauna (1964) in which Antarctica was designated as a ‘Special Conservation Area’. Up until 1991, five categories of protected areas had been designated: Specially Protected Areas (SPAs); Sites of Special Scientific Interest (SSSIs); Historic Sites and Monuments (HSMs); Specially Reserved Areas (SRAs); Multiple-use Planning Areas (MPAs).”[22]

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[20] International Council of Scientific Union

[21] mainly pre-Madrid Protocol

[22] Definition quoted from http://cep.ats.aq/cep/apa/introduction/index.html.

For THIS THESIS, the category SSSI was of relevance, since the preliminary field season as well as the actual study took place in SSSIs. As outlined below, this category and the category SPA were summarily grouped into the category ASPA in 2002, when Annex V of the Protocol of Environmental Protection to the Antarctic Treaty (= Madrid Protocol) eventually came into force. At the time THIS STUDY took place, however, the category SSSI still held true.

2.1.3.1 Definition SSSI (Site of Special Scientific Interest)

> “The purpose of SSSIs is to protect sites where scientific investigations are being carried out or are planned, and there is a demonstrable risk of interference which would jeopardise those investigations, or to protect sites of exceptional scientific interest.
>
> Most SSSIs are protected for a specified period, but the time limit can be reviewed and extended at the ATCM. SSSIs adopted since 1997 are designated for an indefinite period. Each SSSI has a Management Plan which the ATCPs have agreed should be complied with voluntarily.”[23]

As becomes evident, the priority of SSSIs is protection for the purposes of science. While in many cases this may be beneficial to the area’s non-human inhabitants, this is by no means guaranteed.

When the (main document of the) **Protocol on Environmental Protection to the Antarctic Treaty** (= Madrid Protocol) entered into force in 1998 (after having been agreed upon in 1991), it designated Antarctica as a “natural reserve devoted to peace and science” (Article 2), and aimed to provide for comprehensive protection of the Antarctic environment. **Annex V to the Protocol** which entered into force on 24 May 2002 rationalised the existing protected area system by creating two new designations: **ASPAs** (Antarctic Specially Protected Areas) and **ASMAs** (Antarctic Specially Managed Areas). In accordance with the new categories, all SPAs and SSSIs previously designated were incorporated as ASPAs. The sites were renumbered and renamed according to a 3-digit scheme (ASPA 101, 102, 103, etc.) agreed several years earlier and finalised on the XXV Antarctic Treaty Consultative Meeting (ATCM) in Warsaw in September 2002.

2.1.3.2 Definition ASPA (Antarctic Specially Protected Area)

> “Any area, including any marine area, may be designated as an Antarctic Specially Protected Area (ASPA) to protect outstanding environmental, scientific, historic, aesthetic or wilderness values, any combination of those values, or ongoing or planned scientific research.” (Article 3, 1. of Annex V to the Protocol on Environmental Protection to the Antarctic Treaty, as quoted in the 9th Handbook of the Antarctic Treaty System 2002, pp. 58f.)

Article 3 of Annex V to the Protocol on Environmental Protection to the Antarctic Treaty (= Madrid Protocol) goes on to list the various types of ASPAs that are to be included in “the series of Antarctic Specially Protected Areas”. The nine types outlined explicitly (Article 3, 2. a-i) include

- “areas kept inviolate from human interference so that future comparisons may be possible with localities that have been affected by human activities” (Article 3, 2. a),
- “areas with important assemblages of species, including major colonies of breeding native birds or mammals” (Article 3, 2. c),
- and “areas of particular interest to on-going or planned scientific research” (Article 3, 2. e).

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[23] Definition quoted from http://cep.ats.aq/cep/apa/introduction/index.html.

Entry into an ASPA is prohibited except by a permit[24] issued under a Management Plan specified in Article 5 of the same Annex.

2.2 Tourism and Other Human Activities in Antarctica

> "A footprint in the Antarctic moss could last for decades, a plastic pen dropped onto an isolated beach could remain there for centuries, and even a minor oil spill could upset an ecosystem and kill off a rare species of plant or animal." (Masson 1990, as quoted in Hall 1992, p. 5)
>
> "What is needed now is not any further regulations, but a more wholehearted commitment by all Treaty nations to the spirit and not just the letter of environmental protection in Antarctica." (Walton 1987, p. 92)

According to Kriwoken (1991), human activity on continental Antarctica began in 1898, when Borchgrevink[25] first wintered on land, where, he and his team 'lived in the midst of' the Adélie penguin colony at Ridley Beach, Cape Adare, the inhabitants of which formed part of their diet (Austin 1957). Ever since then, humans have been present in the Antarctic for a number of reasons, of which both present-day science and tourism have entered the field fairly late. While Antarctica is often called a continent of science, historically, economics was one of the primary reasons to brace the harsh conditions of Antarctica (White 1994). Looking at the economic history of human presence in the Antarctic, White (1994) recognised several 'waves' in the development (tab. 2-1). He noted (ibid., p. 249) that "despite the efforts of environmentalists, it is clear that all waves of economic activity including the scientific wave, have had heavy impact on the environment".

Antarctic economy was first based on early **exploration**, followed by the commercial development of the **seal and whale industries**. Since 1958, the largest part of the Antarctic economy has been the production of **scientific research**. In terms of the level of science and support expenditures, this continues to be the case, even if since the 1990s **tourists** have outnumbered science and logistic personnel and thus became, in terms of number of people, the most important part of Antarctic economy (White 1994).

For some time, a wave of **'mineral resource exploitation'** (including hydrocarbons, i.e., oil) appeared imminent, as the Convention for Regulation of Antarctic Mineral Resource Activities (CRAMRA) was drawn up and was open to signing 1988/ 1989. It was indeed signed by several governments (including the UK, the US and the then USSR), but subsequently vetoed by Australia and France for environmental reasons, and remains unratified to date.

At present, the **Madrid Protocol on Environmental Protection** to the Antarctic Treaty (signed 1991, entered into force 1998, s.a.), effectively bans mining and drilling activities until its review 50 years after adoption (i.e., in 2041). According to Bauer (1994), the ban on mining and drilling resulted in commercial tourism emerging as the last major commercial activity currently taking place in the Antarctic Treaty area. After CRAMRA had been abandoned, the ATCPs recommenced their discussion of the need for regulation of Antarctica tourism at XXIV ATCM in 2001; and since

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[24] Entry into an ASMA (Antarctic Specially Managed Area) does not require a permit, but activities are directed by a Code of Conduct set out in the Management Plan.

[25] The Norwegian South Polar researcher Carsten Egebert Borchgrevink (1864-1934) was the first to set foot on the Antarctic continent (1895), and overwintered 1898/ 1999 at Cape Adare. Starting out from the Ross Sea region, he [and – presumably – his team] managed to get as far inland as 78°50' (dtv-Lexikon 2006, Vol. 3, p. 300; translation and remark in angular brackets by K.Schuster).

Table 2-1: Historical Development of Antarctic Economy (adapted from White 1994).

Wave	'Economic Focus'	Duration
1	Sealing Period	1780-1892
2	Whaling Period	1919-1942
3	Scientific Period	1943-present
4	New Fishing Period	1970-present*
5	Tourism Period	1993-present
6	'Iceberg-Exploitation' Period (hypothetical)	Future

*regulated by CCAMLR (Convention on the Conservation of Antarctic Marine Living Resources) since 1980/ 81

then, tourism has been a substantive issue at each ATCM, with its own ATCM working group in existence since XXVII ATCM in 2004 (ASOC[26] 2006).

It appears noteworthy that before the onset of commercial tourism, the term 'tourist' had already been employed to characterise a variety of people, as exemplified in Stonehouse (1992, p. 213).

> "Among the Antarctic research community the term 'tourist' was first used as one of mild derision. Expeditioners who overwintered on the continent – once the majority – tended in this way to describe their supposedly less hardy colleagues who visited only in summer. All in turn applied the term semi-jocularly to observers, journalists, reporters, visiting dignitaries, and others on expeditions who were not directly involved in research or support (see, e.g., Stonehouse 1965)."

Both tourism and science have substantially increased during the history of human presence in the Antarctic, raising questions of the extent and justifiability of their respective impacts on the Antarctic environment and its natural inhabitants (e.g., ASOC & UNEP[27] 2005; Giese 1996; Thomson 1977; Wilson, R.P. & al. 1989, 1991; Woehler & al. 1994).

Studies conducted to examine **human impact** on Antarctic birds and mammals have focused on various parameters (behaviour, physiology, breeding success) and levels of enquiry (individuals, populations, ecosystems). While on the individual level, human impact has been compared to that exerted by conspecifics/ congeners or predators (e.g., Culik & al. 1990; Culik & Wilson, R.P. 1991; Giese 1998; Nimon 1997), impacts on animal populations or on ecosystems have used environmental changes (sea ice extent, krill availability, temperature changes) as a comparative basis for assessing impact severity (e.g., Micol & Jouventin 2001). Existing **guidelines** (codes of conduct) include 'intuitive ones' as well as those formulated on the basis of scientific studies. Some of the guidelines drawn up by a variety of organisations are presented below (section 2.2.4).

2.2.1 Trends in Antarctic Tourism

> "Technically, all humans in the history of Antarctica have been tourists, as there are no permanent residents." (White 1994, p. 246)
>
> "Tourists are defined as visitors who are not affiliated in an official capacity with an established National Antarctic Programme." (Enzenbacher 1992b, p. 17)
>
> „In the Antarctic context, tourism is defined as all existing human activities other than those directly involved in scientific research and the normal operations of government bases." (Hall & McArthur 1993, p. 117)

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[26] Antarctic and Southern Ocean Coalition

[27] United Nations Environmental Program

Following ENZENBACHER (1992b), tourist numbers reported here refer to the Treaty Area, i.e., south of 60°S. ENZENBACHER's definition of tourism (ibid.; see quote) includes fare-paying passengers, private expedition members and adventurers aboard sea- or airborne vessels (who actually set foot on Antarctica), but leaves out off-duty Antarctic personnel, official inspection team members, distinguished visitors (DVs, e.g., government representatives, film teams), tour operator crew and staff members as well as passengers (and crew) on Antarctic overflights (that do not 'touch base'). The 'official' Antarctic tourism statistics and trends have been compiled by the International Association of Antarctica Tour Operators (IAATO, see below) and the United States National Science Foundation (NSF) since 1989. Problems arising from ENZENBACHER's definition will be outlined in section 2.2.1.2.

2.2.1.1 History of Antarctic Tourism

> "Tourists generally do not fish, mine, drill or dynamite, nor do they eat penguins." (WHITE 1994, p. 249)
>
> "It would be a large tourist facility indeed that matched the current scale of installations and activities at McMurdo [US], Rothera [UK], or Mawson [AU] stations." (STONEHOUSE 1992, p. 214)
>
> The concept of ecotourism claims that "tourists can become properly informed about, and become particularly sensitive to, the complex and fragile nature of the places which they visit. […] Such claims fall a long way short of being realised" (MÜHLHÄUSLER & PEACE 2001, p. 359).

Commercial tourism activity in Antarctica probably commenced in the mid-1950s (MOSER 2002), but regular annual tourist voyages did not start until 1966 (HEADLAND 1994). Cruise ships have offered a regular basis for tourism since 1966 (CIAPUTA & SALWICKA 1997). The first purpose-designed ship, Lars-Eric Lindblad's 'Lindblad Explorer'[28], completed its first three voyages in 1970, and this year may be regarded as the beginning of the modern period of Antarctic tourism[29] (HEADLAND 1994).

The increase in tourism during the 1990s was largely a result of ice-class vessels from the former Soviet Union becoming available for charter for tourist cruises (MOSER 2002). Around the year 2000, **shipboard cruising** (as opposed to airborne tourism) accounted for over 90 % of Antarctica's tourists (www.antarcticanz.gov.nz). Most tours operate out of Ushuaia (Argentina), Punta Arenas (Chile), or Stanley (Falkland Islands/ Malvinas) (MOSER 2002). To the present, the vast majority of cruises visit the Peninsula region (e.g., ATCM XXIV/IP 2001, UBA 2008[30]), while landings in the Ross Sea area occur much more rarely (e.g., in 2001/ 2002: 3 % of all landings in Antarctica). According to ENZENBACHER (1992b), the **popularity of the Peninsula region** can be attributed to several factors, viz., the proximity and abundance of South American ports, a milder summer climate (compared to elsewhere in Antarctica), diverse and abundant wildlife offering premium photographic opportunities, relative freedom from pack ice for landings (again, compared with other Antarctic locations), and the largest concentration of Antarctic research stations, which represent 'bonus sites' visited by most tour operators. For some time, Arctowski Station (Poland) in Admiralty Bay (King George Island, South Shetland Islands) was the most heavily visited research

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[28] a Norwegian-registered vessel

[29] even though tourism did not attain the character of a 'wave' until 1993 (cf. WHITE 1994; THIS THESIS, tab. 2-1)

[30] homepage Umweltbundesamt

station. In 1992/ 1993, a total of 2996 tourists came ashore on 32 visits, in 1996/ 1997, a ‘mere’ 13 visits yielded a total of 1051 tourists (Ciaputa & Salwicka 1997).

Apart from shipborne tourism, two classes of **airborne tourism** are prevalent in Antarctica, viz., overflights without landing, and flights including landing. According to Swithinbank (1993), landings began in the South Shetland Islands in 1982, when passengers were brought from Punta Arenas by an aircraft of Fuerza Aérea de Chile (Chilean air force); and tourists have been accommodated in a Chilean government hostel since 1983.

“Like **all tourists**, visitors to Antarctica are constantly seeking new experiences, reflected in the changing range of tour activities and destinations” (Moser 2002, p. 42). Among these are, e.g., mountain climbing, snow boarding, kayaking, or marathons to the South Pole (Moser 2002). Many of these activities are pursued further inland so that the respective tourists are somewhat less likely to negatively impact wildlife on the mere basis of fewer encounters, as few animals are found beyond the coastal area. Airborne tourists that actually touch ground, likewise frequently engage in various types of ‘adventure’ or ‘extreme sports’ tourism.

In August 1991, seven tour operators founded the **International Association of Antarctica Tour Operators (IAATO)** (Enzenbacher 1992b). In the same year, they formulated a set of self-imposed guidelines for visitors and tour organisers (box 2-1) comprehensively pulling together information scattered through the existing ATS documents. IAATO has attended ATCM as an observer since 1992 (Enzenbacher 1992b), and in 1994 presented their set of guidelines to the ATCPs which was amended and adopted at the XVIIIth ATCM in Kyoto, Japan (see box 2-2 and box 2-3). By 2000, IAATO included 44 members and associate member companies in 13 countries. Since 2001, IAATO has decided to allow for membership of companies operating vessels with up to 500 passengers. Companies with vessels carrying over 500 passengers[31] are also eligible for membership provided they do not make landings in Antarctica. Industry controls through IAATO include general guidelines, bylaws relating to passenger numbers, landings, visit records, and ongoing improvement of marine safety requirements. (www.antarcticanz.gov.nz)

As of 2010[32], IAATO comprises more than 100 companies, from Argentina, Australia, Belgium, Canada, Chile, France, Germany, Italy, Japan, the Netherlands, New Zealand, Norway, Sweden, the United Kingdom, the United States, and the Overseas Territory-Falkland Islands (Islas Malvinas). IAATO’s four levels of membership include ‘Members’, ‘Associate B 1 Members’, ‘Associate B 2 Members’, and ‘Affiliate Members’[33]. Of the **46 full members**, 33 run ships with a passenger capacity below 200, five companies employ ships with a capacity between 200 and 500 passengers, and four companies are classified ‘cruise-only’ (i.e., no disembarkations). Of the remaining four, two companies offer land-based operations, another one air cruises (no landings), and the last does not specify its mode of operations (private vessels). In terms of nationality, the majority of full members are based in the US (more than 10), followed by Australia, Canada, Germany, Argentina, Chile and the Netherlands (more than three), and a number of countries with one company.

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[31] E.g., in January 2007, ‘MS Golden Princess’ carried 2,425 passengers and a crew of approximately 1,100 (Bertram & al. 2008). No landings were undertaken. As of 2010, IAATO reports 3,000 guest as the maximum number of cruise-by (no landings) passengers (www.iaato.org).

[32] The following facts are taken from http://apps.iaato.org/iaato/directory.

[33] For more information, see iaato-website at apps.iaato.org/iaato/directory.

Box 2-1: Guidelines for Visitors and Organisers of Antarctic Tourist Expeditions as Formulated by IAATO (1991). Phrasing and order taken from Enzenbacher (1992b, p. 21). IAATO = International Association of Antarctica Tour Operators.

Members of IAATO have pledged:

(1) to be knowledgeable of and abide by the Antarctic Conservation Act of 1978 (U.S. Public Law 95-541);

(2) not to enter areas designated as sites of special scientific interest or that need special protection;

(3) to operate only with qualified expedition staff of which at least 75 % must have previous Antarctic experience;

(4) to hire only Zodiac[34] drivers with experience in polar regions;

(5) to educate passengers and crew and enforce the members' self-imposed Antarctica Visitor Guidelines [(s.b.)];

(6) to assign one qualified naturalist staff member to accompany and supervise each group of 20-25 passengers (maximum) ashore;

(7) to cooperate with science stations and not disturb sites of scientific research;

(8) to limit the number of passengers ashore; and

(9) to follow the international MARPOL[35] treaty guidelines regarding marine pollution.

2.2.2.2 Numbers and Trends in Antarctic Tourism

Since the 1990s, tourists have far outnumbered science and support staff engaged in national research programmes (White 1994), although these scientists and other government related visitors tend to spend more time in Antarctica and carry out different types of activities over a wider range of sites (www.antarcticanz.gov.nz).

The steep rise in tourist numbers and trips began in 1985/ 1986 (figs. 2-3, 2-4), and the number of vessels started to increase substantially from 1989/ 1990 onwards (Enzenbacher 1992a). Between 1992 and 2007, the number of available tourism ships excluding yachts has increased from 12 to approx. 40 vessels. Maximum carrying capacities of these ships vary substantially, from just 20 (e.g., 'Sir Hubert Wilkins', 2001/ 2002 season) to 3,100 (Star Princess, running since 2007). As outlined above, ships carrying more than 500 passengers do not make any landings. For the German cruise ships 'Bremen' and 'Hanseatic', IAATO documents give carrying capacities of 164 and 180[36] passengers, respectively (Information Paper at the ATCM XXIV 2001).

According to Murray & Jabour (2004, quoting Tracey 2001) the 1990s saw an escalation of tourism numbers by 800 %[37]. Compared to the early 1990s, the annual number of tourist visits to Antarctica doubled between 1992/ 1993 (6,704 passengers) and 2002/ 2003 (13,571 passengers). Subsequently, it again more than doubled between 2002/ 2003 and 2007/ 2008 (approx. 30,000;

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[34] The rubber boat (Zodiac) as an important means of short-distance transport constituted an important contributing factor to the increase in tourism (Headland 1994).

[35] MARPOL 73/ 78: International Convention for the Prevention on Pollution from Ships as amended by its 1978 Protocol (entered into force 1983).

[36] 188 in the 2010/ 2011 season, according to www.iaato.org, acc. 18.10.2010

[37] N.b.: My attempts to derive at this proportion using figures quoted by IAATO, ASOC, etc. have amounted to a 'mere' 710 % increase...

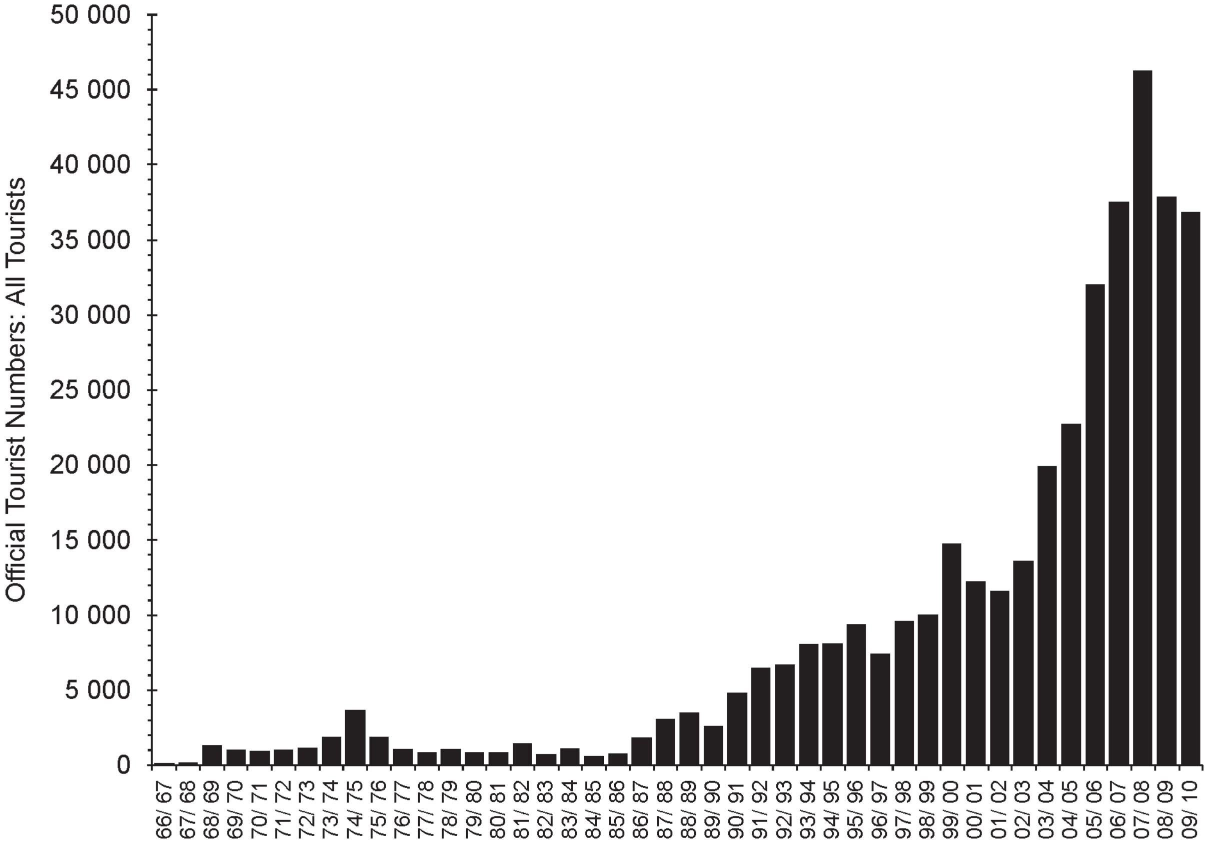

Figure 2-3: Numbers and Trends in Antarctic Tourism between 1966/ 1967 and 2009/ 2010. Figures have been taken from Enzenbacher (1992a, b, 1993, 1994) until 1993, and from IAATO (iaato.org) until 2009/ 10. For discrepancies with respect to figures reported elsewhere, see text.

UBA[38] 2008). Other countries, presumably including passengers that do not leave cruise ships[39], report an even more severe increase in tourism numbers. UK British Antarctic Survey (BAS) lists over 37,000 tourists for the season 2006/ 2007 already; and a US American source (the-world-factbook: www.cia.gov), quoting IAATO, states 30,087 passengers for 2005/ 2006, 36,460 for 2006/ 2007, 46,265 for 2007/ 2008, and 37,858 for 2008/ 209 (all figures excluding overflights). Further discrepancies may arise if 'accompanying non-tourists' (i.e., cruise staff, guides etc.) are included.

It is obvious that at least some of the groups excluded from Enzenbacher's definition (1992b; s.a.) – and thus from 'official' reports – also exert an impact upon Antarctic wildlife. In particular, off-duty logistic personnel of research stations and off-duty staff members and crew of cruise ships could well be considered to take a rather 'touristic' interest in their surroundings. Indeed, the definition provided by Hall & McArthur (1993, s.a.) includes recreational activities of government personnel, and Donachie (1994, p. 335) likewise states that "[o]ff-duty scientific and expedition personnel may be grouped alongside tourists insofar as they also have the potential to adversely affect the Antarctic environment".

Furthermore, figures attain a far more alarming magnitude (as compared to the 'official' tourist numbers presented by IAATO and NSF, see fig. 2-3) whenever attempts are made to include

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[38] Umweltbundesamt

[39] As mentioned above, ships carrying passenger numbers greater than 500, may not 'spill them on the beach'.

[40] Cruise ship personnel comprise the captain, officers, expedition leader and/ or cruise director and staff including naturalists/ lecturers and boat drivers, and all other crew members (Enzenbacher 1992a).

some of these groups. Concerning cruise personnel[40], it was demonstrated for the season 2003/ 2004 that while official tourist numbers came to 24,591[41], the sum of passengers, staff and crew totalled over 43,000 people (ASOC and UNEP 2005).

In any case, the official tourist numbers presented in figure 2-3 have been collected on only the people included in Enzenbacher's definition, and trends in Antarctic tourism are well visible with or without including the other groups.

According to the German Umweltbundesamt (UBA), approx. 30,000[42] tourists actually landed in (i.e., set foot on) Antarctica during the austral summer 2007/ 2008; and figures were assumed to at least remain at that level for 2008/ 2009. As can be seen from figure 2-3, total numbers of tourists have by far exceeded that mark, but these include between 11,000 and 15,000 'cruise-only' passengers. Even though the number of landing sites increased dramatically (e.g., Stonehouse 1992: some 50 sites; Stonehouse 1995: 180 sites), sites suitable for tourist landing are not homogeneously used; e.g., in 2005/ 2006, 85 % (1,178) of all landings occurred at 30 sites only.[43]

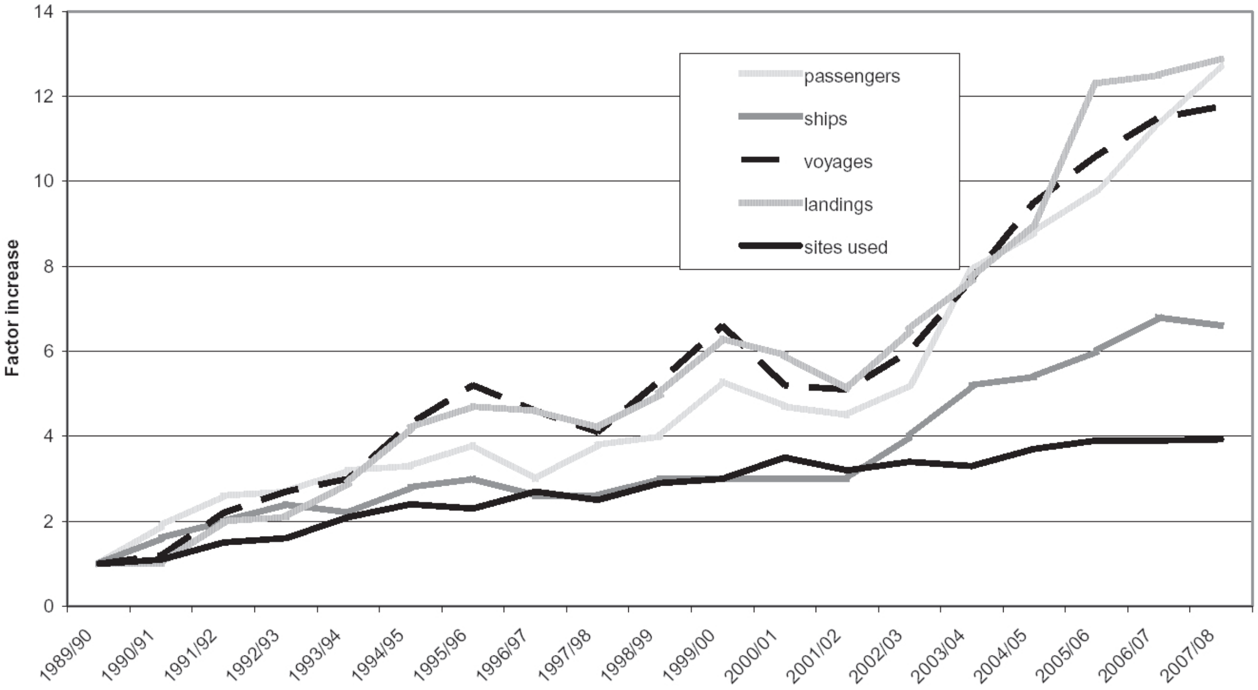

Figure 2-4: Factor Increase in Traditional Landing Shipborne Tourism in the Antarctic Peninsula between 1989/ 1990 and 2007/ 2008. The figure has been taken from Information Paper 82 (IP 82), presented by IAATO at the ATCM XXXI (2008). Compared to passengers, voyages and landings, the increase in landing sites used has been low. The moderate increase in the number of ships partly masks the variability in carrying capacities. **N.b.:** Number of ships does not include sailing or motor vessels carrying 12 or fewer passengers.

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[41] Lee (2005), quoting the same source, reports 24,281 tourists.

[42] including more than 4,000 German tourists

[43] Figures quoted from homepage Umweltbundesamt.

2.2.2 Trends in Scientific Activity

> "The number of signatories to the Antarctic Treaty has grown, research stations continue to increase and expand, access to the Antarctic continues to improve, and the most favourable locations for siting facilities are becoming increasingly scarce." (Harris 1991b, p. 323)

On their homepage[44], The Council of Managers of National Antarctic Programs[45] (COMNAP) list 29 National Antarctic Programmes and a total of 82 stations (year-round plus summer-only). Recent accounts name 40 year-round stations (1 of them German), accompanied by "a range of seasonal-only (summer) stations, camps, and refuges […]; in addition, during the austral summer some nations have numerous occupied locations such as tent camps, summer-long temporary facilities, and mobile traverses in support of research" (the world-factbook: www.cia.gov; May 2009 estimate). The definition of 'summer-only' thus appears to lack stringency, as despite a unanimously acknowledged growth in numbers of stations, Kriwoken (1991, p. 1) referred to a total of "22 nations operating 44 stations and about 45 summer bases in the Antarctic Treaty Area" as early as 1991. For 2009, the world-factbook gave the **winter** population as 1,100 and the **peak summer** population as 4,490 people, with around 40 vessels operating for these programmes. Personnel, including ship's crew and scientist doing onboard research, amount to a further 1,000 people. With respect to the summer population 2008/ 2009, 90 **Germans** were listed, whereas the entire winter population of 2009 included only 9 Germans. The figures presented for approximately 20 years ago (Kriwoken 1991, p. 1) are considerably lower, i.e., around 2,700 and 800 for summer and winter populations, respectively. According to some authors, the overall figures have seen little change up to the early 1990s (e.g., Stonehouse 1992[46]). Harris (1991a, quoting the earlier figures from Headland & Keage 1985), however, states that on King George Island, scientific and support population roughly doubled between 1983 and 1990, and Kriwoken (1991, p. 1) speaks of a "continent-wide increase in station numbers and impact, increasing station size, human numbers, lengths of roads, buildings, waste material production, and energy requirements." Woehler & al. (1994, p. 273) likewise state that "[t]he number of personnel spending the summer at Casey (Australian base) has gradually increased since the station was opened in 1968, and presently totals approximately 70 to 75 people". They go on to say that the rise in numbers of people has led to an augmented use of nearby Shirley Island for both recreational and scientific purposes.

2.2.3 Impact on Antarctic Wildlife

> "There were instances of provocation of Elephant Seals and penguins in order that 'action shots' could be taken. Small groups were also led through rookeries causing disturbances to nesting birds, and one couple were given a box containing three eggs as a souvenir… Insufficient guidance was given on the sensitivity of vegetation on the Antarctic Peninsula, and visitors walked on grass and mosses. One tourist also collected plant specimens." (Codling 1982[47], p. 6, reporting on tourists)

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[44] http://www.comnap.aq

[45] The term was coined prior to the growing presence of tourism and refers exclusively to scientific programmes.

[46] "During every austral summer since the International Geophysical Year 1957-58 several thousand scientists and support staff have worked in Antarctica." (Stonehouse 1992, p. 213)

[47] née Reich, as quoted in Beck (1990b, 1994)

> "Headland (1994[48]) estimated that on the basis of present day figures, less than 1 % of human impacts can be attributed to tourism. The rest comes from scientists and government staff." (Tejedo & Benayas 2006, p. 494)

> "All human activities in Antarctica, whether conducted by scientists, tourists, or others exert environmental impacts." (Beck 1994, p. 380)

As outlined in the previous sections, human activity in general has strongly increased over the last decades. It is reasonable to suppose that tourists (and those engaged in tourist operations) as well as scientists (and their support personnel) may exert an impact on Antarctic wildlife. This section provides a brief summary of potential/ actual impacts for each of the groups.

Comparing the lists provided below, an important **difference between tourists** (including their support personnel) **and scientists** (do.) ought to be kept in mind, viz. their **dissimilar impact on Antarctic wildlife with respect to 'space-time'**: Cruise travel (and other tourist operations) in the Antarctic summer coincides with the peak breeding periods for many species (Hall & McArthur 1993). The main body of tourists will thus impact on a relatively constricted number of sites within a severely constricted period of time – roughly the same time in which many species are 'energetically challenged' due to reproductive duties. In contrast, numbers of scientists and particularly station personnel are stretched over an extended period of time as well as space, although their numbers, too, peak in the summer months.

Impacts that may arise from tourists, their support personnel, cruise ships, and aircraft include the following (e.g., Bauer 1994; Beck 1990b; Ciaputa & Salwicka 1997; Davis 1998, 1999; Hall 1992; Hall & McArthur 1993; Woehler 1997)

- 'blocking' of (unprotected) landing areas by groups of people or tied-up zodiacs (tourists, support personnel)
- noise from humans and/ or zodiac motors (tourists, support personnel)
- increase in intra-specific aggression in, e.g., seals, as animals are forced to form more compact groups when approached too closely (tourists, support personnel)
- increase in predation caused by (groups of) people approaching too closely (tourists, support personnel)
- disruption of breeding cycles, e.g., by flushing breeding birds from their nests (tourists, support personnel)
- disruption of feeding, reproductive or 'socially important' behaviours (tourists, support personnel)
- aggressive pursuit of photographic opportunities (mainly tourists, also accompanying guides, rarely other support personnel)
- feeding, touching, and handling wildlife (tourists, support personnel)
- degradation or eradication of vegetation through footprints (tourists, support personnel)
- discarded litter or garbage[49] (tourists, support personnel)
- alien imports such as plants, animals, and microbes (tourists, support personnel)
- 'inadvertent' entry of protected areas (tourists, support personnel)
- cumulative impacts by multiple cruises serially targeting the same populations (tourists, support personnel, cruise ships)

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[48] p. 279

[49] litter: waste materials, shreds, and fragments scattered about; garbage: household refuse

- inadequate waste and sewage disposal (cruise ships)
- marine fuel leakage, fuel spills (cruise ships)
- fallout from engines (aircraft)
- disturbance of wildlife due to noise of overflights (aircraft)

To date, the majority of impacts directly caused by human presence are explicitly addressed in the **guidelines** (see next section) which are handed to each tourist upon entry of the cruise ship. The tourists' understanding and following these guidelines, however, is not a necessary given. Moreover, enforcement of these guidelines is only as good as the tour guides (can) make it, and may differ according to nationality of tourists or tour operators (Davis 1998). In other cases, it may simply be subject to conditions of terrain, e.g., when strictly adhering to a certain distance from breeding penguins would result in seriously shortening or even abandoning the entire trip (Davis 1998; pers. obs.).

It is interesting to note that for tourists (and support personnel) **reasons for** continuing insensitivity to their potential **impact** are almost identical to those listed below for scientific and support personnel.

The principal difference in attitude appears to be that tourists do not treat Antarctica as 'their own back yard' (see below), but rather feel entitled to full enjoyment of an experience for which they have paid a substantial amount of money and which – in most cases – they will not get a chance to repeat in the foreseeable future.

Impacts effected through scientists, their support personnel, supply ships, and aircraft may include the following (e.g., Beck 1990a, b; Bricher & al. 2008; Donachie 1994; Harris 1991a; Headland & Keage 1985; Müller-Schwarze 1984; UBA[50] 2008; Walton 1987).

- habitat loss through station construction or expansion; airstrip construction
- derelict buildings
- generator exhausts
- noise from aircraft and station; noise from hydro-acoustic measurements
- water contamination
- inadequate waste and sewage disposal
- discarded plastic items, polystyrene and packaging (probably rather from supply ships)
- marine and terrestrial fuel leakage, fuel spills
- marine and terrestrial oil leakage, oil spills
- soil compression through tracked vehicles
- degradation or eradication of vegetation through footprints, vehicle tracks, sampling procedures, etc.
- alien imports (plants, animals, microbes)
- destruction and removal of biota for scientific purposes
- multiple projects targeting the same populations (serially or simultaneously)
- feeding wildlife
- disturbance to wildlife

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[50] Umweltbundesamt

To date, the majority of these impacts have been or are being addressed. **Environmental Impact Assessment** (EIA) is used to decide "on the least disruptive course of action commensurate with particular objectives" (Walton 1987, p. 91), and cleaning procedures have been successfully employed to remove or contain rubbish dumps and noxious materials, resulting in, e.g., the complete removal of the nuclear reactor complex at McMurdo Station (Walton 1987). The introduction of non-native animals has been prohibited since the ratification of Annex II of the Madrid Environmental Protocol[51]. The **Committee for Environmental Protection** (CEP) gives advice and formulates recommendations to parties regarding implementation of the Protocol on Environmental Protection to the Antarctic Treaty and its annexes (Joyner 1996). Unfortunately, CEP is not given any decision-making authority.

Reasons for (continuing) **insensitivity** of scientists and/ or their support personnel **to impacts** have been put forward by a number of authors (e.g., Donachie 1994; Harris 1991a; Riffenburgh 1998; Walton 1987). They include

- lack of adequate training in environmental and conservation principles
- lack of incentive (especially in military personnel who in general have no personal motivation for being in the Antarctic)
- treating Antarctica as their backyard 'because they live there'
- not feeling bound by treaty provisions through lack of enforcement
- cultural differences concerning environmental perceptions, priorities and approaches to management

While some of the impacts listed above are clearly 'task-related', a number of them overlap with reservations expressed towards tourism. Moreover, scientific and logistic personnel have the potential to negatively influence tourist behaviour (e.g., Riffenburgh 1998). Codling[52] (1982, as quoted in Hall 1992, pp. 6f.) argued that further attention should be given to environmental education for station workers, as their behaviour "seemed to cause great environmental disturbance, and through their example adversely affected tourists".

With respect to the scientific concern regarding the rising number of tourists and the increasing demands of the tourism industry, Donachie (1994) strongly advocates management and regulations but advises his fellow scientists (ibid., p. 342) as follows.

> "A cautionary note to scientists, however, is that one must be wary of adopting a 'holier than thou' attitude vis-à-vis the increasingly vocal 'lobby' to control purely tourist visits to Antarctica. One should not need to be reminded of the environmental effects of past, and even present, scientific research, and activities conducted in its name. Steps must be taken to 'put our own house in order', and ensure that one on- or off-duty scientist or technician, does not demonstrate the destructive capacity of the 'feared tourist hordes'".

For the purposes of this study, no distinction was made between tourists, off-duty personnel and on- or off-duty scientists, as the intention was to **investigate the direct impact of human presence and activity** on incubating penguins. The discussion section will, however, reflect on the relevance of the findings reported with respect to the different 'users' of Antarctica. An overview of studies examining a variety of aspects of human impact on penguins will be presented below (section 2.3.2.1, tab. 2-7).

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[51] The Madrid Protocol on Environmental Protection to the Antarctic Treaty states in its Annex II (Conservation of Antarctic Flora and Fauna), Article 4 (Introduction of Non-Native Species, Parasites and Diseases) that dogs "shall not be introduced onto land or ice shelves and dogs currently in those areas shall be removed by April 1, 1994" (4.2.).

[52] née Reich, an author who had previously worked on the development of Antarctic tourism

2.2.4 Guidelines for Human Conduct Towards Antarctic Wildlife

> “The guidelines are, by and large, principles of common sense to which general related information has been added. It is forbidden to use aircraft, small boats, or vessels in ways that disturb wildlife. This is conceptually useful but offers no practical advice on how to avoid disturbing wildlife.” (Davis 1999, p. 518 referring to Recommendation XVIII-1 and IAATO guidelines)

> “We consider minimum approach distance guidelines should be based on the separation distance necessary to allow animals to undertake normal activity, rather than on the distance people can approach wildlife before the animals flee.” (Holmes & al. 2005, p. 339)

Like all other activity, tourism and private expeditions in Antarctica fall under the provisions of the Antarctic Treaty and subsequent recommendations and protocols agreed by member countries.

The primary instruments are **Recommendation XVIII-1**[53] (a.k.a. Kyoto Recommendation) and the provisions of the **Madrid Environmental Protocol**. Other legal instruments, such as **CCAMLR**[54], also apply. In 1994 (ATCM XVIII in Kyoto, Japan), the Antarctic Treaty Parties adopted Recommendation XVIII-1 within the context of implementing the Madrid Protocol on Environmental Protection to the Antarctic Treaty.

Originally developed by IAATO (International Association of Antarctica Tour Operators), **Recommendation XVIII-1** provides guidelines for **visitors** (‘Guidance for Visitors to the Antarctic’, box 2-2; for full text, see appendix 2-1) as well as **organisers** of tourist expeditions (‘Guidance for Those Organising and Conducting Tourism and Other Non-Governmental Activities in the Antarctic’, box 2-3; for full text, see appendix 2-1).[55]

> “The Environmental Protocol applies to tourism and non-governmental activities as well as governmental activities in the Antarctic Treaty Area.” (Handbook of ATS 9th ed. 2002 Tourism and Other Non-Governmental Activities)

Although guidelines are aimed at all visitors to the Antarctic, including tourists, crewmembers, scientists and support personnel (see quote; Enzenbacher 1992a), Recommendation XVIII-1 is generally taken to address tourists and tour operators, while government employees are expected to comply with the rather ‘implicit’ guidelines which are more or less scattered through the ATS. Riffenburgh (1998, p. 193) stated that

> “the military and support personnel have not had a specific set of established rules [comparable to IAATO guidelines; Recommendation XVIII-1], although they have been expected to be in compliance with the requirements of the Protocol on Environmental Protection to the Antarctic Treaty and national legislation. […] The government personnel can therefore ‘break’ many of the specific guidelines that tourists follow.”

Possibly for just that reason, a number of countries took care to develop or specify their own guidelines (e.g., Germany, UK, USA, and Australia). Additionally, Management Plans for a number of sites have drawn up site-specific guidelines regulating all human activities (e.g., Heard and Macquarie Islands, Australia). After some disputes concerning the relative importance of national/ site-specific vs. IAATO guidelines (e.g., Woehler 1997), IAATO acknowledged the sovereignty of

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[53] The Kyoto Recommendation (= Recommendation XVIII-1) is not sufficient to stop unwanted change “if the Antarctic Treaty Consultant Parties have not decided what is unwanted.” (Davis 1999, p. 531)

[54] Convention on the Conservation of Antarctic Marine Living Resources (1980/ 1982)

[55] www.antarcticanz.gov.nz

such more specific guidelines. IAATO's revised Marine Wildlife Watching Guidelines (IAATO 2007) state that "[s]ome countries have guidelines or regulations stricter than these which may override IAATO's guidelines." The organisation takes care to remind their tour operators that they should be aware that

> "compliance with the IAATO guidelines might be insufficient to prevent violation of, and penalties resulting from, national laws and regulations." (IAATO 2007, unpaginated)

Table 2-2 presents an overview of general guidelines proposed by various authors and sources.

Table 2-2: Examples of Guidelines. ATCM: Antarctic Treaty Consultative Meeting; COMNAP: Council of Managers of National Antarctic Programmes; IAATO = International Association of Antarctica Tour Operators; SCAR = Scientific Committee on Antarctic Research; UBA = Umweltbundesamt.

Target Group	(Journal of) Publication	Target Area	Author	Year
Antarctic Visitors	website Umweltbundesamt	Antarctica	UBA	2002 2009
	COMNAP website	Antarctica	COMNAP	1993
	Oceanites Foundation Polar Record	Antarctica	NAVEEN & al.; reviewed by STONEHOUSE	1989 1990
Antarctic Tourists & Tour Operators	IAATO website	Antarctica	IAATO	2007
	IAATO website Annals of Tourism Research	Antarctica	IAATO; reviewed by SPLETTSTOESSER & FOLKS	1992 1994
Aircraft Operators	Biological Conservation	Antarctica	HARRIS	2005
	Final Report XXVII ATCM	Antarctica	ATCPs (modified & less stringent version of SCAR recommendation)	2004
	Marine Ornithology	Antarctica	SCAR	2000
Arctic Visitors	Tourism Management	Arctic	MASON	1994

Box 2-2: Guidance for Visitors to the Antarctic as Outlined in Recommendation XVIII-1 (Excerpt). Boldface has been added by the author of this thesis.

A) PROTECT ANTARCTIC WILDLIFE

1) **Taking or harmful interference** with Antarctic wildlife is **prohibited** except in accordance with a permit issued by a national authority.
2) **Do not** use aircraft, vessels, small boats, or other means of transport in ways that **disturb wildlife**, either at sea or on land.
3) **Do not** feed, touch, or handle birds or seals, or approach or photograph them in ways that cause them to **alter their behavior** [sic]. Special care is needed when animals are breeding or moulting.
4) **Do not damage plants**, for example by walking, driving, or landing on extensive moss beds or lichen-covered scree slopes.
5) Do not use guns or explosives. **Keep noise to the minimum** to avoid frightening wildlife.
6) **Do not bring non-native plants or animals** into the Antarctic (e.g. live poultry, pet dogs and cats, house plants).

B) RESPECT PROTECTED AREAS

C) RESPECT SCIENTIFIC RESEARCH

D) BE SAFE

E) KEEP ANTARCTICA PRISTINE

Box 2-3: Guidance for Those Organising and Conducting Tourism and Other Non-Governmental Activities in the Antarctic as Outlined in Recommendation XVIII-1 (Excerpt). Boldface has been added by the author of this thesis.

KEY OBLIGATIONS ON ORGANISERS AND OPERATORS

1) **Provide prior notification of, and reports on, their activities** to the competent authorities of the appropriate Party or Parties.
2) Conduct an **assessment of the potential environmental impacts** of their planned activities.
3) Provide for **effective response to environmental emergencies**, especially with regard to marine pollution.
4) Ensure self-sufficiency and safe operations.
5) **Respect** scientific research and the Antarctic **environment**, including restrictions regarding protected areas, and the protection of flora and fauna.
6) **Prevent the disposal and discharge of prohibited waste**.

PROCEDURES TO BE FOLLOWED BY ORGANISERS AND OPERATORS

A) When planning to go to the Antarctic

B) When in the Antarctic Treaty Area

C) On completion of the activities

D) Antarctic Treaty System Documents and Information

Guidelines often involve **minimum approach distances (MAD)** and/ or buffer areas. Regarding these, one of the problems guidelines face is their relative generality (see quote by Davis 1999 above). With respect to Antarctic wildlife, this has led to either the exclusion of any distance-related advice (e.g., COMNAP[55] guidelines), or the (scientifically untenable) setting of the same minimum approach distance for a variety of different species (e.g., IAATO guidelines, but see 'Leitfaden für Besucher der Antarktis', UBA 2002, 2009) regardless of differences in 'flightiness', vulnerability, breeding stage, etc. As early as 1998, a specialist group meeting in Jena[56] , Germany, suggested that minimum approach guidelines ought to be species-specific and pointed out that the animals' responses differed in the course of their breeding cycle and the subsequent moulting period. As recent as 2005, however, Holmes & al. (2005, p. 340) observed that

> "[t]he 5 m minimum approach distance is often applied as a blanket guideline, applicable to all penguin species during all stages of their breeding and moult […]".

To be successful, minimum approach distances would thus have to be **species-specific** (e.g., Ellenberg & al. 2006), frequently **site**-specific, **time**-specific (e.g., breeding stage, moult), and **impact-modulated** (i.e., more tourists might require to be kept further away, e.g., Beale & Monaghan 2004a). The minimum approach distance problem is further aggravated by the fact that in practice, at a number of sites it is not always possible to maintain even the prescribed distances due to terrain or narrow access to features of interest (Davis 1999, Enzenbacher 1992a).

Tables 2-3 a) to c) illustrate the considerable amount of variability with respect to minimum approach distances suggested by various authors and sources.

Additionally, table 2-3 shows that most guidelines also advise people to seek to **minimise impact by observing** the animals' **behaviour**. This approach would be promising, if descriptions of the types of behaviour/ behaviour changes indicating 'disturbance' were included. These, however, are generally lacking, and misinterpretations have been observed to occur even with respect to some of the authors of these guidelines: The brochure of the German Umweltbundesamt 'Leitfaden für Besucher der Antarktis' (Guidelines for Antarctic Visitors, UBA 2002), for instance, contained a photograph (p. 3) showing Adélie penguins in various stages of increased vigilance and apprehension (expressed by wide eyes, displaying the white sclerae, and raised flippers) or agonistic behaviours (Sideways or Alternate Stares), while the subtitle interpreted the penguins' behaviours (or at least that of the vigilant/ apprehensive front penguin) as 'welcoming the visitors'. The error has been eliminated in the meantime, and the photo does not appear in the 2009 brochure. Nevertheless, this goes to show that even the most well-intentioned agencies may err. **True minimisation of human impact might be achieved**, **if** comprehensive **descriptions** of behaviours/ behaviour changes found to be **indicative of** an animal's **'disturbance' could be provided** to those potentially causing said 'disturbance'. Identification of indicative behaviours was one of the aims of this thesis (see aims in section 2.4).

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[55] Council of Managers of National Antarctic Programmes

[56] Workshop on 'Human Impact on Antarctic Mammals and Birds'. Institut für Polarökologie, Jena, 04/ 05 May, 1998

Table 2-3 a): Variations in Minimum Approach Distances (MAD). A: Penguins. acc.: accessed; excl.: excluding; AAD: Australian Antarctic Division; IAATO = International Association of Antarctica Tour Operators; SWHI, Jena: Scientific Workshop on Human Impacts; Jena, Germany; UBA = Umweltbundesamt.

Target Birds	**MAD**	**Additional Information**	**Scientific Study Quoted**	**Recognisable Parameters for Tourists**	**Author**	**Year**
Penguins	4.5 m	Gentoos more sensitive than Chinstraps; penguins with eggs or chicks more easily disturbed than moulting birds	none explicitly quoted	changes in activity; break of activity	IAATO	1992
	5 to 10 m	increase distance if changes in behaviour are observed	none explicitly quoted	changes in activity; break of activity	IAATO	2007
	5 m	no rings (of people) around penguins; no blocking of paths (Right-of-Way)	lack of scientific database; urgent need for studies; MADs should be species-specific	none explicitly provided	SWHI Jena	1998
Penguins (excl. Emperors)	5 m	increase distance if changes in behaviour are observed; physiol. param. might change even in the absence of beh. changes	none explicitly quoted	changes in behaviour	UBA	2002
Penguins in Colony (excl. Emperors)	10 m	increase distance if changes in behaviour are observed; physiol. param. might change even in the absence of beh. changes	none explicitly quoted; but results from study by Giese (1998) reported	interruption of breeding, desertion of young	UBA	2009
Breeding/ Moulting Penguins (excl. Emperors)	30 m	increase distance if signs of disturbance are detected; if wildlife approaches of its own accord, remain as still and quiet as possible until birds move away	none explicitly quoted	signs of disturbance	AAD	acc.: 2008
Breeding/ Moulting Emperor Penguins	50 m	increase distance if signs of disturbance are detected; if wildlife approaches of its own accord, remain as still and quiet as possible until birds move away	none explicitly quoted	signs of disturbance	AAD	acc.: 2008
Emperor Penguins within colonies	30 m	increase distance if changes in behaviour are observed; physiol. param. might change even in the absence of beh. changes	none explicitly quoted	changes in behaviour	UBA	2002, 2009

Table 2-3 b): Variations in Minimum Approach Distances (MAD). B: Albatross, Skuas, Giant Petrels. acc.: accessed; AAD: Australian Antarctic Division; IAATO: International Association of Antarctica Tour Operators; SG: South Georgia; SWHI, Jena: Scientific Workshop on Human Impacts; Jena, Germany; UBA: Umweltbundesamt.

Target Birds	MAD	Additional Information	Scientific Study Quoted	Recognisable Parameters for Tourists	Author	Year
Nesting Albatross (SG)	10 m	increase distance if changes in behaviour are observed	none explicitly quoted	changes in activity; break of activity	IAATO	2007
Displaying Albatross (SG)	25 m	increase distance if changes in behaviour are observed	none explicitly quoted	changes in activity; break of activity	IAATO	2007
Albatrosses	100 m	increase distance if signs of disturbance are detected; if wildlife approaches of its own accord, remain as still and quiet as possible until birds move away	none explicitly quoted	signs of disturbance	AAD	acc.: 2008
Skuas	20 m	increase distance if signs of disturbance are detected; if wildlife approaches of its own accord, remain as still and quiet as possible until birds move away	none explicitly quoted	signs of disturbance	AAD	acc.: 2008
	situation -specific	reatreat when attack flights start	scientific expert experience	attack flights	SWHI Jena	1998
Giant Petrels	100 m	none	scientific expert experience	none explicitly provided	SWHI Jena	1998
	100 m	increase distance if signs of disturbance are detected; if wildlife approaches of its own accord, remain as still and quiet as possible until birds move away	none explicitly quoted	signs of disturbance	AAD	acc.: 2008
	50 m	increase distance if changes in behaviour are observed	none explicitly quoted	changes in behaviour	UBA	2002, 2009
	25-50 m	increase distance if changes in behaviour are observed	none explicitly quoted	changes in activity; break of activity	IAATO	2007

Table 2-3 c): Variations in Minimum Approach Distances (MAD). C: Other Seabirds. acc.: accessed; excl.: excluding; AAD: Australian Antarctic Division; IAATO = International Association of Antarctica Tour Operators; SWHI, Jena: Scientific Workshop on Human Impacts; Jena, Germany; UBA = Umweltbundesamt.

Target Birds	**MAD**	**Additional Information**	**Scientific Study Quoted**	**Recognisable Parameters for Tourists**	**Author**	**Year**
All Nesting Birds	4.5 m	increase distance if changes in behaviour are observed	none explicitly quoted	changes in activity; break of activity	IAATO	1992
All Nesting Birds excl. Albatross, Giant Petrels	4.5 m	increase distance if changes in behaviour are observed	none explicitly quoted	changes in activity; break of activity	IAATO	2007
All Seabirds excl. Giant Petrels	15 m	increase distance if changes in behaviour are observed	none explicitly quoted	changes in behaviour	UBA	2002
Seabirds (no specification)	15 m	increase distance if changes in behaviour are observed	none explicitly quoted	warning calls, attack flights (terns, skuas)	UBA	2009
Non-breeding Birds	5 m	increase distance if signs of disturbance are detected; if wildlife approaches of its own accord, remain as still and quiet as possible until birds move away	none explicitly quoted	signs of disturbance	AAD	acc.: 2008
Antarctic Terns	situation-specific	retreat when alarm calls are heard	scientific expert experience	alarm calls	SWHI Jena	1998
Petrel; Breeding Prion	20m	increase distance if signs of disturbance are detected; if wildlife approaches of its own accord, remain as still and quiet as possible until birds move away	none explicitly quoted	signs of disturbance	AAD	acc.: 2008
Sheathbills, Cormorants; Other Seabirds	5m	none	scientific expert experience	none explicitly provided	SWHI Jena	1998

2.3 Human Impact on Animals

> “The monitoring of human impacts is a fundamental part of Antarctic logistics and must become a routine part of Antarctic station operations.” (ATCM XXIX 2006, p. 6)
>
> “It is not the wilderness that must be controlled, but the human activity within it.” (Davis 1999, p. 524)

With respect to the design of THIS STUDY, two areas of research have been influential on different levels. For the behavioural and physiological parameters used, the wealth of information provided by **animal welfare science** was consulted, while the approach to operationalising human disturbance under field conditions corresponded more closely to the discipline of **conservation behaviour**. Following, the two fields are briefly outlined, before more detailed information is provided on the parameters measured and the concept of human disturbance used.

2.3.1 Animal Welfare Science

> “You don’t have to be very clever to feel pain. Nor do you have to be a great intellectual to feel hunger or even fear”. (Dawkins 1997, p. 63)
>
> “The rise in public interest in animal welfare during the past two decades[57] has been dramatic. Concern for animals is evident throughout society in many countries and is invisible only to those who do not want to see.” (Broom & Johnson 2000, p. 2)

In the introduction to an Animal Welfare Course at the University of Cambridge, UK, Prof. D.M. Broom[58] (11 September, 2005) stated that **issues concerning animal protection** have long predated the scientific study of animal welfare. Cruelty to dogs and horses was in the focus of public concern during the 19th century up until the 1950s. From the 1950s until the early 1980s, campaigns against experiments on laboratory animals received much public attention; and since the 1960s, welfare concerns have been increasingly extended to include farm, companion, zoo and wild animals.

Animal welfare science as a research field has originated in veterinary medicine in the late 1960s, and nowadays draws upon various areas of expertise in Veterinary Science, Biology and Psychology. According to Dawkins (2005/ 2006, p. 77), it represents “the most comprehensive of all the biological sciences”, embracing animal behaviour, evolution, behavioural ecology, neuroscience, genetics, cognitive science, “and even consciousness studies”. Since approximately 2005, smaller-scale laboratory studies are increasingly complemented by large-scale on-farm research; and meta-analyses of already published data (evidence-based approach, e.g., Sutherland & al. 2004) are likewise on the rise.

2.3.1.1 Animal Welfare Science – Definitions and Concepts

> Broadly speaking, the science of animal welfare asks **three big questions**:
>
> Are animals conscious? How can we assess good and bad welfare in animals?
>
> How can we use science to improve animal welfare in practice? (Dawkins 2005/ 2006, p. 77)

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[57] Given the fact that the 1st edition was published in 1993, we have by now well passed the 3-decade line.

[58] Colleen Macleod Professor of Animal Welfare at the Department of Clinical Veterinary Medicine, University of Cambridge, UK

Animal welfare is about as easy – or difficult – to define as is human welfare. **Good welfare** starts with **physical health**, but it requires more than that, for it also implies that animals have **positive** (pleasure, contentment) rather than negative **emotions** "such as fear or frustration, which we humans label 'suffering'" (Dawkins 2005/ 2006; p. 77).

Broom (1986, 1988a, b) **defined** the welfare of an individual as

> **"its state as regards its attempts to cope with its environment"**.

It is important to notice that the definition is phrased in such a way that it "refers to a characteristic of the individual at the time" (Broom & Kirkden 2004, p. 2).

Coping in this context means to have control of mental and bodily stability (Broom & Johnson 2000) which includes normal regulation of body state as well as emergency responses.

The "state as regards attempts to cope" refers to both how much has to be done in order to cope with the environment and the extent to which coping attempts are succeeding (Broom & Johnson 2000, p. 74). There are various methods used by individuals who try to counteract adverse effects or difficult conditions. Attempts to cope include a variety of **behavioural** responses, as well as emergency **physiological** responses, the functioning of body repair systems and **immunological** defences.

Extreme examples of indications of (prolonged) failure to cope are impaired life expectancy and reduced ability to reproduce (Broom & Johnson 2000). If the failure to cope is only short-term (e.g., danger-induced adrenal activity for a limited period), it is unlikely to result in impaired life expectancy, but it does cause poor welfare with respect to the individual concerned. Likewise, the absence of fitness reduction does not automatically suggest good welfare: Wiepkema (1985, as quoted in Broom & Kirkden 2004, p. 3) lists pain, fear, and difficulty controlling interactions with the environment (e.g., because of overstimulation or too much unpredictability) as welfare-reducing aspects which do not necessarily have an impact on biological fitness. And Wechsler (1995, p. 131) states:

> "From an evolutionary perspective adaptation has failed when there is a reduction in biological fitness, i.e., in the number of offspring. This type of argumentation is, however, not sufficient to judge animal welfare. **Ultimate causes** of behaviour have to be differentiated from **proximate causes** (Dawkins, 1983; Wechsler, 1993). The animal's behavioural organisation is directed at proximate goals which are only correlatively related to the ultimate functions of behaviour. Therefore, what matters for the animal is to reach these proximate goals and coping behaviour represents a set of strategies that, at least in a natural environment, increase the probability of attaining such goals."

If an animal's coping systems succeed only with difficulty (taking much time and energy), welfare of that animal is poor during the process (Broom 1988b), and may remain poor until complete recovery has been achieved.

In determining an animal's welfare state at a given time, the assessment of physical health is relatively straightforward, but the 'emotional part' of the requirements (see above) has proved far more difficult to tackle.

Addressing this problem, one of the main types of study in animal welfare science focuses on examining **animal emotions**. These studies use a variety of ways of 'asking' animals what they do and do not want. **Preference tests**, in which animals are given a choice of aspects of their environment and the outcome is monitored, were first employed by Hughes and Dawkins (e.g., Hughes 1975 quoted in Duncan 2006; Dawkins 1977), and have since then been ridded of certain pitfalls associated with them (e.g., choices deleterious to the animal's health). According to Duncan (2006) preference tests give a good first indication of what the animals feel about various aspects of their environment.

As a follow-up to preference tests, studies measure the **strength of the preference**, for instance, by 'increasing the price the animal is willing to pay' (i.e., testing how hard the animal will work to achieve their goal). '**Obstruction tests**' may involve pushing past an obstruction or pushing open a weighted door (e.g., Nicol & Guildford 1991; Mason & al. 2001), while in '**operant responding**' the strength of the animals' motivation is measured in terms of 'just how often they will repeat an action' they have learnt to associate with a reward (e.g., Dawkins & Beardsley 1986). **Evidence** from such studies strongly suggests that animals do have preferences and are generally prepared to work for them.

A further fact arising from these investigations concerns the frequently high inter- and intra-individual as well as situational variability of preferences. Although these laboratory or on-farm studies are not easily transferred to the field setting, the important take-home message would seem to be that **individuals might have to be considered individually**.

Moreover, if animals are acknowledged to have preferences and be able to indicate them in a 'graded' fashion (i.e., stronger preference for this, weaker preference for that within a given set of circumstances), it seems reasonable to assume the animals equally capable of expressing a **gradation with respect to disturbing stimuli** (e.g., conspecific disturbance, different types of human visitation).

Animal welfare scientists have given much attention to the concept of **stress** (e.g., Broom & Johnson 2000; Broom & Kirkden 2004; Fraser & Broom 1990; Koolhaas & al. 1999; von Borell & al. 2007). Measurements of stress responses have involved a variety of parameters, e.g., behaviour, heart rate, the adrenal axes and other hormones (review in Broom & Johnson 2000). Broom & Johnson (ibid., p. 178) **define stress** as being

> "an environmental effect on an individual which overtaxes its control systems and reduces its fitness or appears likely to do so. Fitness reduction involves increased mortality and failure to grow or reproduce".

Fitness is measured as lifetime reproductive success. It should be noted that (fitness evaluations being outside the scope of THIS THESIS) the term '**stressor**' is used in a broader context here (like, for instance, in Tarlow & Blumstein 2006/ 2007; see section 2.3.3), referring to stimuli that cause measurable disturbance responses but do not necessarily permit predictions with respect to ultimate fitness consequences.

Some of the important points Animal welfare science is making have contributed to THIS THESIS. The conceptual fact that **welfare is a characteristic of an animal** (e.g., Fraser & Broom 1990), not something given to it, emphasises the relevance of **individual-based approaches** to the assessment of the impact of human disturbance on animals.

Research on **coping strategies** and **styles**, i.e., different responses to the same (aversive) stimulus (e.g., "escape, remove[59], search, wait[60]": Wechsler 1995; "proactive vs. reactive": Koolhaas & al. 1999; Wingfield 2003) has demonstrated that both **species-specific strategies** (e.g., responses

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[59] including increased aggression

[60] including apathetic behaviour

of prey species vs. predator species) and **individual-specific responses** have to be taken into account when investigating human impact. As Broom (1988b, p. 16) states:

> "Each individual animal has several alternative methods of trying to cope with adversity and individuals differ in the methods which they favour."

With respect to stress, Jordan (2005, p. 518) points out: "Scientists argue that stimuli with which the animal can cope are essential to keep the coping process in good working order, and the dividing line between what is beneficial and what is harmful varies for each individual."

The concept pursued by animal welfare science also introduces a measure more sensitive and more readily accessible than lifetime reproductive success and/or its components (e.g., life expectancy and inclusive fitness), employing **proximate measures** like behavioural and physiological parameters (e.g., Broom & Kirkden 2004; Dawkins 1997, 2003, 2005/ 2006; Duncan 2005; Mendl 2001).

In doing so, the concept challenges the assumption that negative human impact on animals can be considered inconsequential as long as the overall population remains 'on the right side of extinction'[61].

The validity and applicability of various behavioural and physiological parameters in the **assessment** of animal welfare have been **reviewed** by a number of animal welfare scientists (tab. 2-4). Even though the respective studies have been conducted on laboratory or farm animals, the conclusion that **there is no single measure of welfare** (e.g., Broom & Johnson 2000; Dawkins 2005/ 2006; Swaisgood 2006/ 2007) is transferable to field conditions. Jordan (2005), for instance points out the problems of wild animals 'masking' injuries, and of different species reacting to the same stimulus in different ways. Swaisgood (2006/ 2007, p. 141) likewise notes that "no single measure provides the 'silver bullet' for understanding welfare" and stresses the necessity to monitor a "suite of behavioral [sic] variables in concert" (ibid.) to characterise an animal's state.

This has led to the inclusion of both a broad array of behavioural parameters as well as one physiological (i.e., heart rate) parameter in this thesis.

2.3.1.2 Animal Welfare Science – Behavioural Measures of Disturbance

> "The most obvious indicator that an individual is experiencing difficulty in coping with a problem is often a behavioural response. […] The best indicators of long-term problems for an animal are frequently measurements of behaviour." (Broom & Johnson 2000, pp. 88, 130)
>
> "[U]ltimately a species' behavioral [sic] response to humans will influence its ability to coexist with humans." (Tarlow & Blumstein 2006/ 2007, p. 430)

Behavioural responses to stimuli in general can be broadly categorised into **three classes**[62]:

1. Behaviours seen <u>only</u> or <u>predominantly during</u> exposure to a given stimulus.
2. Behaviours <u>no longer/ more rarely</u> seen <u>during</u> exposure to the given stimulus.
3. <u>Changes</u> in behaviour <u>after</u> exposure to the stimulus.

---

[61] The opposite suggestion, viz., that disturbance has sufficiently negative effects only if the species/ population as a whole is endangered, has been put forward by some researchers (e.g., Nisbet 2000).

[62] Weary & al. (2006) use a classification like this for behavioural responses to pain.

Table 2-4: Reviews on Behavioural and Physiological Parameters Used in the Assessment of Animal Welfare (in Reverse Chronological Order). Small font size indicates taxa occasionally mentioned, while main study animals are represented by larger font size. Only taxa named in the main body text/ in tables have been listed. Beh.: behavioural; Physiol.: physiological; anim.: animal(s).

Author(s)	Year	Parameters		Topic of Review (Taxon, if applicable)
		Beh.	Physiol.	
vonBorell & al.	2007	–	x	Heart Rate Variability for Assessing Stress and Welfare mammals: pigs, cattle, sheep, goats, horses; birds: poultry
Weary & al.	2006	x	x	Identifying and Preventing Pain mammals: humans, laboratory animals (lab mice/ rats), dogs, cats, cattle (esp. calves), sheep, pigs, elk, deer; birds: hens/ broilers
Kirkden & Pajor	2006	x	–	Preference, Motivation and Aversion Tests mammals: pigs, rats, mink; birds: hens
Broom & Kirkden	2004	x	x	Welfare, Stress & Pathophysiology mammals: tree shrews, domestic ungulates, horses, rats, mice; birds: chickens/ hens, junglefowl, starlings, canaries
Broom & Johnson	2000	x	x	Stress & Animal Welfare mainly domestic mammals and birds
Koolhaas & al.	1999	x	x	Coping Styles: Current Status in Behaviour and Stress Physiology mammals: humans, rhesus monkeys, domestic ungulates, tree shrews, beech martens, mice, rats; birds: chickens, great tits; fish: sticklebacks, rainbow trouts; invertebrates: octopi
Rushen	1996	x	(x)	Aversion Learning Techniques to Assess Mental State, Suffering and Welfare of Farm Anim. mammals: domestic ungulates, horses; birds: hens
Wechsler	1995	x	(x)	Coping and Coping Strategies – a Behavioural View mammals: rats, mice, bank voles, tree shrews, pigs, calves, dogs, polar bears, mink; birds: hens, barbary doves
Boissy	1995	x	x	Fear and Fearfulness mammals: vervet monkeys, olive baboons, marmosets, squirrel monkeys, dogs, domestic ungulates, deer, rabbits, California ground squirrels, rats, mice; birds: black-billed magpies, domestic fowl, Japanese quails
Bateson	1991	x	x	Assessment of Pain mammals: humans, chimpanzees, dogs, cats, horses, rats; invertebrates: insects, cephalopods
Rushen	1991	x	x	Problems Associated with the Interpretation of Physiological Data in the Assessment of Animal Welfare mammals: pigs, other domestic ungulates; birds: hens
Barnett & Hemsworth	1990	x	x	Validity of Physiological and Behavioural Measures of Animal Welfare; Focus on Problems Concerning Behavioural Measures mammals: pigs, other domestic ungulates, horses; birds: poultry
Rushen	1986	x	–	Validity of Behavioural Measures of Aversion mammals: domestic ungulates, rats, dogs; birds: pigeons

The third class of responses includes both **long-lasting changes** in behaviour and the short-term **'recovery time'** before normal behaviour is again exhibited.

Incorporation of all three classes into THIS THESIS was effected by a **three-period-design**, comprising behaviour prior to, during, and after visitation.

It is stressed that for all three classes, knowledge on what constitutes **'normal' behaviour** (i.e., behaviour in the absence of a given stimulus, prior to exposure) is paramount (e.g., BATESON 1991; BROOM 2001; MAYER 2007). For this, the animals' general **'response repertoire'** (i.e., their evolutionary history = phylogenetic constraints) as well as possible or actual **current constraints** of this repertoire need to be taken into account, e.g.,

- climatic: possibility of preferential behaviours to be shown for different temperatures/ wind conditions etc. [63];
- topographical: angle of stimulus presentation or height difference to stimulus presented, available space to respond;
- annual: stage of breeding cycle;
- ontogenetic s.l.: physical maturity and learning processes;
- individual: body condition, temperament/ personality/ character

The general 'response repertoire' is best obtained by **ethograms**, either from the literature or in preliminary studies, whereas some current constraints prove more difficult to tackle, particularly those pertaining to individual animals (i.e., body condition, learning, and personality).

Measurements can be obtained with respect to the **intensity**[64] (qualitative) or **magnitude** (quantitative), **duration** and **frequency** of responses, the **cessation** of 'normal' behaviour, the **delay** before normal behaviour is resumed and, under some circumstances, the effects of **social facilitation**[65] (BROOM & JOHNSON 2000).

In THIS THESIS, behaviour responses to disturbance were quantitatively[66] evaluated with respect to **rate** (relative frequency) and/ or **duration**, while **intensity** was examined qualitatively. For selected behaviours, **reduction**/ **cessation** during, and **delay** after disturbance were quantified to investigate their disturbance specificity.

The **'flow'** of behaviour before, during, and after disturbance was assessed to examine changes in overall performance. In this context, 'flow' combines the duration of expressing behaviours belonging to a given behaviour system with occurrence and 'smoothness' of transitions between systems. Taken together, these components are referred to as the animal's **behavioural topography** (for details see chapter 4.3.2.4.6).

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[63] with probable links to metabolism (e.g., energy conservation) and self-preservation (e.g., heat reduction)

[64] With respect to within-parameter comparisons, this term is used a) when referring to initial differential degrees of expression (e.g., among groups pre-visit), or b) to degrees of changes without specifying exact magnitudinal values (e.g., for a gradually increasing intensity in agonistic behaviours: Bill-to-Axilla, Sideways Stare, Alternate Stare, Point, Gape). Concerning between-parameter comparisons, resting behaviour is awarded the lowest degree of intensity, while vigilance and particularly agonistic behaviours are considered behaviours of high intensity.

[65] The term social facilitation refers to behaviour that is initiated or increased in rate or frequency by the presence of another animal carrying out that behaviour. (FRASER & BROOM 1990, p. 391)

[66] magnitudinal changes

2.3.1.3 Animal Welfare Science – Physiological Measures of Disturbance

> “Monitoring heart rate is a sensitive and precise way to measure human impact. Incorporating measures of cardiac response with behavioral [sic] observations can identify the specific events that affect animals. […] Cardiac measurements can be a powerful tool to detect how individuals respond to specific stressors and are uniquely able to document how long it takes them to recover from a particular disturbance.” (Tarlow & Blumstein 2006/ 2007, p. 442)

Physiological parameters used to assess animal welfare (reviewed in Broom & Johnson 2000), include **heart rate**, **respiratory rate**, **body temperature**, and the **adrenal axes** (hormonal stress response). A tabulated summary of the review is provided below (tab. 2-5). While the first three parameters are more or less self-explanatory, adrenal axes are briefly explained in box 2-4.

Box 2-4: The Adrenal Axes (Broom & Johnson 2000; Harvey & al. 1984). ACTH: adrenocorticotropic hormone; AM: adrenal-medullary system; CRF/ CRH: corticotropin-releasing factor/ hormone; HPA: hypothalamic-pituitary-adrenal cortex system; Am.E.: American English

The **adrenal axes** comprise two different systems, viz., the **adrenal-medullary system**[67] (AM) with the catecholamines adrenaline (Am.E.: epinephrine) and noradrenaline (Am.E.: norepinephrine), and the **hypothalamic-pituitary-adrenal cortex system** (HPA, s.b.).

According to some authors (e.g., Broom & Johnson 2000), both systems are used to **‘ready the body for emergency action’**, providing more glucose (AM; → to facilitate muscular activity and tissue repair) and more amino acids and fatty acids (HPA; → extension and amplification of catecholamine effects; responsible for later stage of adaptation).

Others (e.g., Harvey & al. 1984 referring to Munck & al. 1984) argue that “the role of the adrenals during stress is not to augment but to **prevent the defence mechanisms from overreacting**, since they can themselves cause damage and endanger survival if activated for too long”.

The first stage of activity in the **HPA** is interleukin-1β-stimulated secretion of corticotropin-releasing factor or hormone (CRF/ CRH). CRF can be measured in the hypothalamus, albeit “only in very restricted experimental conditions” (Broom & Johnson 2000, p. 96).

CRF is the principal agent[68] initiating release of adrenocorticotropic hormone (ACTH) from the anterior pituitary (anterior adenohypophysis).

Via the bloodstream, ACTH is carried to the adrenal cortex, where it serves to release the glucocorticoids[69] (corticosterone, cortisol, or both).

Glucocorticoids inhibit the production of both CRF and ACTH, and ACTH is removed quickly from the blood.

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[67] also called sympatho-adreno-medullary system (DeBoer & al. 1990), sympathetic-adrenal medullary system (McCarty & al. 1988)

[68] Broom & Johnson (2000, p. 96f.) additionally mention catecholamines, the neurohypophysial hormones arginine-vasopressin and oxytocin.

[69] The major glucocorticoid hormone in birds is corticosterone (e.g., Cockrem & al. 2009).

Following, **characteristics of the parameters** potentially relevant to THIS STUDY are briefly described. As measurements in the hypothalamus (see box 2-4) were clearly out of the question (invasive, requiring immobilisation of animals), characteristics of CRF will not be dwelt upon. Whenever penguin physiology might deviate from that of lab/ farm animals, specific penguin studies are quoted. Any non-referenced statements have been taken from BROOM & JOHNSON (2000).

All physiological parameters (tab. 2-5) used in animal welfare lack **context-specificity**, that is, changes have been measured in both aversive and pleasurable contexts. With respect to the adrenal axes, for instance, DEBOER & al. stated as early as 1990[70] that

> "[i]t has been clearly established that acute exposure to *arousing or stressful* stimuli is accompanied by increased sympatho-adreno-medullary and pituitary-adrenocortical activity, resulting in raised plasma concentrations of the catecholamines (CAs), adrenaline (A) and noradrenaline (NA), and of the glucocorticoid corticosterone (CS)."

This fact points to the importance of simultaneous behaviour observations for the interpretation of physiological results, as these help put physiological responses into context (DAWKINS 2003).

Likewise, all parameters are **influenced by** the animal's **activity** as well as by **emotions** (e.g., pain, fear, fright, aggression, frustration). Therefore, separation of motor from emotional components is paramount regardless of choice of parameter.

Immediacy of response after presentation of a stimulus differs between parameters: It is instant for heart rate and for the adrenal-medullary system (1-2 s), 'within one minute' for respiratory rate, 'within minutes' for body temperature and ACTH (adrenocorticotropic hormone), and 'after at least 2 min' (BROOM & JOHNSON 2000) or 1-2 min (ROMERO & REED 2005[71]) for glucocorticoids. With respect to glucocorticoids, however, earlier authors reported considerably more rapid response times: Quoting BEUVING & VONDER (1978), SIEGEL (1980) states appearance of glucocorticoids in domestic chickens to start as quickly as 45 s after onset of restraint (= aversive stimulus) followed by a six-fold increase within 8 min.

Delay of waning of response during- or post-stimulus likewise differs among parameters: While elevated heart rate, respiratory rate, and body temperature have been found to decline more slowly (several minutes to half an hour), adrenaline and noradrenaline (AM) are removed very quickly: BROOM & JOHNSON (2000) quote a half-life in rats of 70 s, while NATELSON & al. (1981) mention 1-3 min for the same species. ACTH is inhibited by glucocorticoids and is quickly removed from the blood so that samples must be taken within a few minutes of the event whose effect is being assessed. In rhesus monkeys, peak ACTH response occurred after 15 min, followed by a steady decline despite pervading conditions afterwards. With respect to glucocorticoids, DEBOER & al. (1990) showed that in rats, corticosterone levels peaked after 15 min in response to handling and novelty of surroundings, and had dropped to almost pre-measurement levels at the next measuring point half an hour later. In response to water immersion, however, corticosterone levels rose steeply during administration of stimulus, but continued to rise after the stimulus was withdrawn, resulting in even higher levels measured half an hour later[72].

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[70] italics added in THIS STUDY

[71] "These results indicate […] that samples collected in less than 2 min reflect unstressed (baseline) concentrations, and that samples collected from 2-3 min also will likely reflect baseline concentrations but at worst are near baseline [i.e., so near that they may still be used as a baseline for subsequent comparisons]." (ibid. abstract, p. 73)

[72] As measuring points were 'few and far between', it is not possible to say whether peak responses lay between end of stimulus and 30 min post-stimulus or between 30 min and 75 min post-stimulus.

Pronounced diurnal fluctuations are mentioned for core body temperature, adrenaline and noradrenaline (DeBoer & van der Gugten 1987), and HPA. For the latter, the cycle in baseline adrenal cortex activity strongly influences response intensity. Culik & al. (1989) did not find a clear pattern of periodicity with respect to penguin heart rate. The same study reported **susceptibility to climatic conditions** for penguin heart rate: Heart rate increased linearly with wind speed but was unrelated to ambient temperature, humidity, cloud cover and estimated solar radiation. Climatic influence has likewise been found for respiratory rate, body temperature, ACTH (increase in cold temperatures – though not in hot, Jeronen & al. 1976), and glucocorticoids (increase in inclement weather, Wingfield 1984). As for adrenaline and noradrenaline (AM), susceptibility to ambient temperature was found in, e.g., pigeons (Jeronen & al. 1976).

Given the different target tissues/ organs, **methods for obtaining measurements** vary in their degree of invasiveness, with observation (respiratory rate) being the least invasive. For penguin heart rate, a variety of apparatus are used, ranging from implants (highly invasive: pre- and post-experimental operations required) and external ECG recorders (highly to moderately invasive: some ‘tie’ the penguin to the recording box) to artificial eggs (least invasive for HR: pre- and post-experimental approach, but no handling or restriction required). Body temperature in penguins has been measured by implanted devices (necessitating pre- and post-experimental operations) or by taking rectal temperatures (handling for each measurement). Measurements concerning the adrenal axes require blood sampling (AM: intravascular canule, handling and insertion of permanent device; ACTH and glucocorticoids[73]: handling for each measurement), urine sampling (AM: catheterisation, handling and insertion of permanent device, results very variable; glucocorticoids: with considerable delay), faecal sampling (of glucocorticoid metabolites, with considerable delay), or saliva sampling (glucocorticoids: much variation).

Blood samples must be taken within the minimum response time for each parameter to avoid measuring disturbance caused by the procedure itself rather than the disturbance stimulus investigated (Broom & Johnson 2000, Romero & Reed 2005).

According to Cockrem & al. (2009, p. 158), “capture, followed by the collection of blood samples over 30-60 min is a widely used stressor in studies of corticosterone in birds […]. The increase in plasma corticosterone concentrations whilst birds experience the stressors is termed a corticosterone response […].” The same authors state that, even though corticosterone responses had been found to differ markedly between individuals, variation in corticosterone responses had not been quantified in free-living birds up until 2009.

In situations of stress, the general **direction of change** for all parameters, (be they cardiac, respiratory, temperature-related or humoral) is ‘up’. One exception to this is found in species exhibiting a ‘freeze’ response (heart rate decrease). Furthermore, peripheral body temperature (but not core body temperature) may decrease.

While respiration rate was initially included as a possible physiological parameter for THIS STUDY, measurements effected by binoculars were soon found too unreliable to include, as focal animals/ groups were located approximately 25-30 m away from the investigator outside visiting experiments, and birds were frequently prone or turned away from the observer.

Of this array of physiological parameters, **heart rate** was thus considered the most feasible and reliable with respect to **suitability for THIS STUDY** (unrestrained animals in the field in maritime

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[73] According to Broom & Johnson (2000), plasma ACTH levels respond earlier than plasma glucocorticoid levels.

Antarctica, hands-off, non-invasive protocol). This decision was much later confirmed by field-related evaluations undertaken by Tarlow & Blumstein (2006/ 2007).

Table 2-5: Comparison of Selected Characteristics of Physiological Parameters Used in the Assessment of Animal Welfare. Parameters clearly dependent on surgical procedures (e.g., measurement of CRF) have been omitted from the table.

Parameter/ Attributes of Parameter	**Heart Rate**	**Respiratory Rate**	**Body Temperature**	**Adrenal Axes: 1. Adrenal-medullary system (AM)**	**Adrenal Axes: 2. Hypothalamic-pituitary-adrenal cortex system (HPA)**	
				Catecholamines: Adrenaline/ Noradrenaline	**ACTH (Adrenocorticotropic hormone)**	**Glucocorticoids (Corticosterone/ Cortisol) in plasma**
Context-specific	no	no	no	no: 'readying the body for emergency action, both positive and negative'		
Activity-related	yes	yes	yes	yes		
Emotion-related	yes	yes	yes, e.g., 'protest': increase; 'despair': decrease	e.g., in humans more passive response: adrenaline; more active/ aggressive response: noradrenaline	yes	
Immediacy of Response after Stimulus Presentation	immediate	within 1 min	within minutes	within 1 s or 2 s	release primarily initiated by CRF, also by catecholamines; appears within minutes (guinea pig: significant increase after 4 min)	release initiated by ACTH; appears after at least 2 min/ 1-2 min
Delay of Disappearance of Response during- or post-Stimulus	may be longer if little behavioural response or much locomotory activity is shown	longer	longer	shorter-lived than HPA; half-life in rats: 70 s	longer-lived than AM; release inhibited by glucocorticoids; removed quickly from blood; rhesus monkey: peak incr. after 15 min, then decline despite pervading conditions	longer-lived than AM; peak towards end or even after stimulus administration
Pronounced Diurnal Fluctuation	no (penguins: Culik & al. 1989)	no	core: yes	yes, in conjunction with behavioural activity (rats)	yes: cycle in baseline adrenal cortex activity	yes: cycle in baseline adrenal cortex activity
Susceptibility to Climatic Conditions	yes (penguins): increase with wind speed (Culik & al. 1989)	yes: increase with ambient temperature	yes (penguins) increase with ambient temperature (Boyd & Sladen 1971)	yes: increase in high and low temperatures	yes: increase in low temperatures	yes: e.g. increase in inclement weather
Measurements Obtained by	implants, external ECG-recorders, artificial eggs	direct observation	rectal thermometer, implanted devices	blood sampling (intravascular canule, immediately after stimulus); urine sampling (catheterisation, and very variable)	blood sampling (within a few mins)	blood sampling (within 2 min); urine-sampling (with considerable delay); saliva (variable); faecal concentrations of glucocorticoid metabolites (with considerable delay)
General Direction of Change	tachycardia (increase); exception: species with a 'freeze' response	increase	core: increase; periphery: may decrease	increase		
Suitability for This Study	high	limited	none	none		

Heart rate measurements in penguins have been employed by a number of studies (also see chapter 3.1.5.2, Table 3-3 and Table 3-4). As early as 1989, Culik & al. reported that Adélie penguins exhibited tachycardia (elevated heart rate) in response to human disturbance, especially to being handled (capture and restraint).

Tachycardia is considered a reaction physiologically preparing the animal for the possibility of flight or fight, and the magnitude of the response is often taken to represent an animal's assessment of the degree of threat to which they are exposed (Price & al. 1993). If tachycardia is to be considered a meaningful physiological response to disturbance stimuli, however, care must be taken to distinguish between increases in heart rate due to **motor activity** and those due to perception of, and reaction to, disturbance, i.e., the **'emotional response'** (Broom & Johnson 2000). Using a heart rate measuring device which only records heart rate when the penguin is sitting quietly, viz., an artificial egg, serves to separate the former from the latter so that elevations can be attributed to 'emotional response' alone. It is acknowledged that it is not permissible to simply extrapolate the (cardiac) reaction of incubating birds to other stages of the breeding cycle (Wilson, R.P. & al. 1991), let alone to the non-breeding period.

To account for individual variation in resting heart rate as well as for susceptibility to climatic conditions, it is recommended that for the assessment of heart rate reactions, **each individual serve as their own control** (Baldock & Sibly 1990). This is effected by comparing a given individual's heart rate responses during disturbance to records obtained immediately prior to disturbance (undisturbed/ pre-treatment 'baseline') of the same individual.

In this thesis, heart rate was examined (for details see chapter 4) as regards

- extent of tachycardiac (increase) responses during disturbance (human, conspecific),
- overall pattern changes during disturbance (human, conspecific),
- delay until resting levels were reached again,
- extent of fluctuations outside disturbance ('baseline sessions'),
- parallelity or complementarity with respect to behavioural indicators.

2.3.2 Conservation Behaviour

> "For those unfamiliar with the term, 'conservation behavior' [sic] is an emerging discipline in applied animal behavior where behavioral research is used as a tool to solve conservation problems." (Swaisgood 2006/ 2007, p. 140, quoting Blumstein & Fernández-Juricic 2004)
>
> "Conservation behaviour is a young discipline that investigates how proximate and ultimate aspects of the behaviour of an animal can be of value in preventing the loss of biodiversity." (Buchholz 2007, p. 401)

When the multidisciplinary field of **conservation biology** was 'founded' by M.E. Soulé in 1985, behavioural biology was not included, nor was behavioural study incorporated into the first conservation biology textbooks (Buchholz 2007; Caro 1999, 2007).

According to Caro (1999, p. 366; 2007, p. 394), conservation biology originally combined principles of population ecology, population genetics and systematics (traditional and molecular techniques) "to study how populations and their habitats respond to anthropogenic change, and now applies this knowledge through protection, restoration and political leverage". Its aim could thus be summarised as the **preservation of species and ecosystems**.

At this time, behaviour scientists were perceived (e.g., CARO 2007; LINKLATER 2004) as either interested in all four of TINBERGEN's (1963) questions[74], but predominantly conducting their experiments inside laboratories and other artificial surroundings (animal behaviour science; focus: proximate as well as ultimate), or as doing field-work and using interesting predictive[75] models, but exclusively looking for adaptive or survival value (behavioural ecology; focus: predominantly ultimate). In the 1990s, scientists from conservation as well as behaviour began to search for ways of integrating behavioural studies into conservation biology, enumerating areas and research questions that would benefit from the cooperation (e.g., SUTHERLAND 1998, DAWKINS 2005/ 2006). They also pointed out, however, the specific weaknesses (as outlined above) behaviour science would have to overcome in order to make a significant contribution to the aims of conservation (see reviews in ANGELONI & al. 2007/ 2008; CARO 1999; LINKLATER 2004).

In short, the aim of **conservation behaviour** is to take 'the best of animal behaviour science and behavioural ecology combined'. Conservation behaviour scientists (e.g., BLUMSTEIN & FERNÁNDEZ-JURICIC 2004) as well as conservation scientists interested in this field (e.g., BUCHHOLZ 2007; CARO 1999, 2007; LINKLATER 2004) stress the importance of looking at **proximate** (immediate causation and ontogeny) as well as **ultimate** (survival value and evolution) questions in order to best decide about conservational measures.

True to one of its 'parents', viz., behavioural ecology, conservation behaviour continues to make extensive use of models, optimality models among them. Optimality theory has been thoroughly criticised (e.g., GOULD & LEWONTIN 1979; PIERCE & OLLASON 1987), amended and re(de)fined (e.g., MCNAMARA & HOUSTON 1980, 1985; OATEN 1977), and it certainly pays to keep firmly in mind the inherent limitations of models – as some of their 'original inventors' seem to indeed have done: MAYNARD SMITH (1977, p. 632), for instance, suggested that the main role of models (in evolutionary biology) "is to help us to see whether, in particular cases, the proposed causes (i.e. selection pressures) are sufficient to account for the observed results". And in another paper (MAYNARD SMITH 1978, p. 35, italics in quote), he further justified the use of optimality principles by pointing out that "[…] in testing a model we are *not* testing the general proposition that nature optimizes but the specific hypotheses about constraints, optimization criteria and heredity". Looking at overall usage[76], however, scientists seem to have frequently left these cautions behind. Almost thirty years later, SUTHERLAND (2006, p. 599) stated that (in conservation) the

> "conventional approach of making assumptions and deriving models to make predictions about the consequences of environmental change is often unsatisfactory for complex problems with considerable uncertainty".

Given the broadened focus (i.e., the 'complete Tinbergen') of conservation behaviour, and judging from reviews (tab. 2-6), scientists in this 'relatively fresh' field appear to critically reassess the validity of the models' assumptions (e.g., BEDNEKOFF & LIMA 1998; LIMA & BEDNEKOFF 1999) as well as their applicability to and suitability for the problem at hand (BLUMSTEIN & al. 2005; TARLOW & BLUMSTEIN 2006/ 2007).

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[74] Augmenting HUXLEY's "three major problems of Biology" by adding ontogeny, TINBERGEN (1963) proposed that the following four questions should be studied by ethologists: 1. causation (physiology; causative mechanism); 2. survival value (adaptive value, function); 3. ontogeny (development); and 4. evolution (phylogeny). He (1963, p. 411) "believe[d] with HUXLEY that it is useful both to distinguish between them and to insist that a comprehensive, coherent science of Ethology has to give equal attention to each of them and to their integration".

[75] but see PIERCE & OLLASON (1987) for a critical assessment

[76] also see GOULD & LEWONTIN (1979) concerning the readiness to entertain non-adaptive explanations, epiphenomenalism of current utility, etc.

On the basis of this development, the **antipredator model** outlined below is considered a viable framework for the assessment of human disturbance.

Table 2-6: Reviews Concerning Methods and Models Used in Conservation (Behaviour in Reverse Chronological Order). a.o.: among others

Author(s)	Year	Method/ Model	Topic of Review
TARLOW & BLUMSTEIN	2006/ 2007	breeding success, mate choice, fluctuating asymmetry, flight initiation distance, immunocompetence, glucocorticoids, cardiac response	evaluating methods to quantify anthropogenic stressors on wild animals, assessing for each method its ease of use, precision in quantifying impact, accuracy in predicting presence, absence, or population viability, and repeatability across populations and species
SUTHERLAND	2006	extrapolation, experiments, phenomenological models, game-theory population models, expert opinion, outcome-driven modelling, scenarios	methods predicting ecological consequences of environmental change
BEDNEKOFF & LIMA	1998	antipredator vigilance	randomness, chaos and confusion in the study of antipredator vigilance
LIMA & DILL	1990	predation – risk assessment	behavioural decisions made under the risk of predation (review of PULLIAM 1973)
ELGAR	1989	predator vigilance & group size	critical review of empirical evidence (a.o. PULLIAM 1973)
YDENBERG & DILL	1986	economics of flight distance	economics of fleeing from predators
HART & LENDREM	1984	vigilance and scanning patterns	improving upon PULLIAM's (1973) model of feeding and vigilance in birds

2.3.2.1 Conservation Behaviour – Effects of Human Disturbance on Birds

> “The problem of human disturbance to nesting seabirds seems to be increasing, and it involves diverse groups of people: recreationists, tour groups, local residents and scientists alike.” (ANDERSON & KEITH 1980, p. 66)
>
> „The dominant management issue must be the management of acceptable […] uses, rather than the identification of appropriate […] users.“ (MCKERCHER 1996, p. 574)

The area of conservation behaviour research particularly relevant to THIS THESIS is that of the impact of **non-lethal human disturbance to animals**. Concerns about the effects of human disturbance upon birds have been increasingly raised since the 1970s (e.g., ANDERSON & KEITH 1980, review and details for Brown pelicans, *Pelecanus occidentalis californicus*; ELLISON & CLEARY 1978 for Double-crested cormorants, *Phalacrocorax auritus*; FROST & al. 1976 for Jackass penguins, *Spheniscus demersus*; GILLET & al. 1975 for Glaucous-winged gulls, *Larus glaucescens*; HAND 1980 for Yellow-footed western gulls, *Larus occidentalis livens*; OELKE 1978 for Adélie penguins, *Pygoscelis adeliae*; OLLASON & DUNNET 1980 for Fulmars, *Fulmarus glacialis*; ROBERT & RALPH 1975 for Western gulls, *Larus occidentalis*; also see review by CARNEY & SYDEMAN 1999).

Initially, the impacts mentioned were either directly related to **scientific research**[77] (e.g., REID 1968) or resulted from **'socioeconomic conflicts'** between humans and animals, such as fisheries or 'guano-harvesting'. The increase in **recreational demands**, however, soon became an additional factor of concern. 'Early birds' in this field reported disturbance on specific colonies or species (e.g., for Adélies: OELKE 1978; REID 1962, 1968; STONEHOUSE 1965, quoted in THOMSON 1977, p. 1178; STONEHOUSE 1967; THOMSON 1977), but already in 1982, BAUER & THIELCKE (quoted in NEEBE & HÜPPOP 1994, p. 8) considered [human] disturbances to be the main factor responsible for the endangered status of 41 of the 78 bird species red-listed in the Federal Republic of Germany at that time. A number of publications on a variety of species have followed (e.g., BURGER & GOCHFELD 1991; BURGER & al. 1995; ERIZE 1987; HÜPPOP & HAGEN 1990; KELLER 1989; NEEBE & HÜPPOP 1994; NIMON & STONEHOUSE 1995; WOEHLER & al. 1994), and to date concern has not abated (e.g., for non-penguins: DEVILLIERS & al. 2005, 2006; FERNÁNDEZ-JURICIC & SCHROEDER 2003; MÜLLNER & al. 2004; WEIMERSKIRCH & al. 2002; reviews: CARNEY & SYDEMAN 1999; NISBET 2000; SCAR 2008; journal supplements: IBIS Supplement 1, March 2007: Recreational disturbance on birds).

With respect to penguins, a total of 50 studies which scientifically investigated or directly reported on disturbance were reviewed for THIS STUDY. A further 15 studies that mentioned disturbance but did not particularly focus on it were likewise used to gather information. An overview of disturbance-related penguin studies is shown below (table 2-7; the unabridged and quite unwieldy table is found in appendix 2-2), and details on their respective findings will be summarised for behavioural and physiological responses reported.

2.3.2.1.1 Behavioural Responses of Penguins to Human Disturbance

N.b.: An ethogram of Adélie penguin behaviour during the breeding period is provided in chapter 3.1.4.

Increased vigilance in response to human visitation has been found for Adélie penguins, *Pygoscelis adeliae* (AINLEY 1974; CULIK & al. 1989, 1990a; GIESE 1998), Gentoo penguins, *P. papua* (NIMON 1997; HOLMES 2004, 2007; HOLMES & al. 2005/ 2006, 2007/ 2008), Royal penguins, *Eudyptes schlegeli* (HOLMES 2007; HOLMES & al. 2005, 2007/ 2008), King penguins, *Aptenodytes patagonicus* (HOLMES 2007, HOLMES & al. 2007/ 2008), Emperor penguins, *A. forsteri* (BURGER & GOCHFELD 2007), and African penguins, *Spheniscus demersus* (VANHEEZIK & SEDDON 1990; DEVILLIERS & GIESE 2004).

Additionally, GIESE & RIDDLE (1999) reported a 100 % increase in vigilance for Emperor penguin chicks during helicopter presence.

An **increase** in **agonistic behaviours** during human visitation is mentioned for Adélie penguins (GIESE 1998), Royal penguins (HOLMES 2007; HOLMES & al. 2007/ 2008), King penguins (HOLMES 2007, HOLMES & al. 2007/ 2008), Magellanic penguins, *Spheniscus magellanicus* (YORIO & BOERSMA 1992; FOWLER 1999, WALKER & al. 2006), Humboldt penguins, *S. humboldti* (ELLENBERG & al. 2006), and African penguins (DEVILLIERS & GIESE 2004).

With respect to Gentoo penguins, findings differ: NIMON (1997) observed threat behaviours towards conspecifics (high threat) and skuas (low threat), but not towards humans, while HOLMES & al. (2007/ 2008) report increased agonistic behaviours during human visitation.

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[77] which, particularly in the (sub-)Antarctic, tends to come with a variable amount of logistical and/or infrastructural requirements (station construction and maintenance, helicopter and ship traffic) and for the early expeditions included killing penguins to provide fresh meat for both sledge dogs and humans

Additionally, Wilson, R.P. & al. (1991) observed agonistic behaviours (head waving) in Adélie penguins during aircraft approach.

Changes in **breeding behaviour** (including standing up, shifting on nest, and nest abandonment) during human visitation were found for Adélie penguins (Giese 1998), Magellanic penguins (Fowler 1999), and African penguins (Hockey & Hallinan 1981; DeVilliers & Giese 2004).

Holmes & al. (2005) observed no nest abandonment in Royal penguins. For Yellow-eyed penguins, *Megadyptes antipodes*, Ratz & Thompson (1999) found no differences in pattern of chick feeding sequences between an unvisited area and one frequented by well-regulated tourism.

Additionally, helicopter landings and aircraft operations were observed to cause abnormal change-over patterns between pairs of nesting penguins (Wilson, R.P.& al. 1991), an interruption of breeding routines through scattering of birds, and exposure of eggs and chicks (Thomson 1977), as well as crèche scattering (Oelke 1978) in Adélie penguins.

Posture changes (‘getting up’) in response to human approach/ presence have been observed for Adélie penguins (Ainley 1974, Giese 1998), Emperor penguins (Burger & Gochfeld 2007), Magellanic penguins (Yorio & Boersma 1992), Humboldt penguins (Ellenberg & al. 2006), and African penguins (Hockey & Hallinan 1981; vanHeezik & Seddon 1990).

Flight behaviour of incubating and/or commuting birds and **scattering** of adults and/or crèches during human approach/ presence has been reported for Adélie penguins (Wilson, R.P. & al. 1991), and African penguins (Hockey & Hallinan 1981; DeVilliers & Giese 2004), but not for Royal penguins (Holmes & al. 2005). For Emperor penguins (Burger & Gochfeld 2007), path deviations at first sight of humans have been observed.

Additionally, flight behaviour and/or scattering in response to aircraft have been mentioned for Adélie penguins (Thomson 1977; Oelke 1978; Culik & al. 1989, 1990a; Wilson, R.P. & al. 1991), and – albeit in a milder form – for Emperor penguin chicks (Giese & and Riddle 1999).

Increased occurrence of **headshakes** during human visitation has been reported for Adélie penguins (Ainley 1974; Giese 1998). For this species, Ainley (1974) also found an increase in **rapid-wing-flaps** during human presence, while Giese & Riddle (1999) mention increased **rapid- and slow-wing-flaps** in Emperor penguin chicks during aircraft presence.

In Adélie penguins, Ainley (1974) additionally observed the following behavioural responses to human and skua disturbance: increase in **ruffle-shakes** and **both-wings-stretches** for skua as well as human presence at 5-10 m, increase in **sneezing** rate during visitation, and decreases in these parameters post-visit. Additionally, **yawns** decreased post-visitation without prior increase.

Findings on **preening** behaviour appear to differ between species: Ainley (1974) states that preening behaviour of visited Adélie penguins did not change during, or after, visitation. In contrast, preening behaviour of African penguins (Hockey & Hallinan 1981) ceased during approach, while that of Gentoo penguins increased, particularly 5-10 min post-visit (Holmes & al. 2005/ 2006, 2007/ 2008).

Concerning Little blue penguins, *Eudyptula minor*, Giling & al. (2008) reported a general **avoidance** of human contact in the publicly accessible breeding area examined.

In contrast, Snares crested penguins, *Eudyptes robustus*, showed **hardly any behavioural response** to human presence (Ellenberg & al. 2004).

With respect to Magellanic penguins (Yorio & Boersma 1992; Fowler 1999; Walker & al. 2006), differences between penguins ‘used to human presence’ and those unaccustomed to it are frequently emphasised. Likewise, Cevasco & al. (2001) report stronger behaviour responses in Magellanic penguins unfamiliar with frequent visitation.

2.3.2.1.2 Physiological Responses of Penguins to Human Disturbance

Increased heart rate in response to human visitation/ presence has been reported for Adélie penguins (Culik & al. 1989, 1990a; Giese 1998; Wilson, R.P. & al. 1991), Gentoo penguins (Nimon 1997), Royal penguins (Holmes & al. 2005), Humboldt penguins (Ellenberg & al. 2006), and African penguins (DeVilliers & al. unpubl. data). According to Ellenberg & al. (2004), Snares crested penguins exhibited **no** heart rate **response** if humans stayed outside the colony; and even upon approach to within 2 m, not all birds examined would show a significant heart rate change. Adélie penguin adults (Culik & al. 1989, 1990a; Wilson, R.P. & al. 1991) and chicks (Culik & al. 1989, 1990a) were found to respond far more strongly to capture than to ‘mere’ human visitation.

As for Adélie penguins, Giese (1998) found heart rate responses to conspecifics or skuas to be lower than those exhibited towards humans at a distance of 5 m. With respect to Gentoo penguins, Nimon (1997) reported increased heart rate to conspecific disturbance in the immediate vicinity of the nest, as well as to prolonged skua encounters. Concerning Humboldt penguins, Ellenberg & al. (2006) noted that heart rate elevations in response to natural stimuli (e.g., conspecifics) returned to resting heart rate levels within seconds (vs. > 30 min post-visitation by humans).

Additionally, elevated heart rate in response to helicopter approach and overflight was mentioned by Culik & al. (1989, 1990a) and Wilson, R.P. & al. (1991) for both Adélie penguin adults and chicks. As for adults, however, figures differ considerably: While Culik & al. (1989, 1990a) reported heart rates of 145 bpm (beats per minute) to helicopter at 20 m altitude, Wilson, R.P. & al. (1991) give a value of 287 bpm for helicopter approach up to 25 m.

Increased body temperature was observed in Adélie adults and chicks (Boyd & Sladen 1971) in response to handling, and to witnessing capture in another penguin, although raised temperatures were not found in all chicks (ibid.: one chick showed no temperature rise after 2 min of handling). It was likewise found in Emperor penguin adults and chicks as a response to handling (Boyd & Sladen 1971) as well as to various man-induced stimuli, direct handling/ weighing, and to a lesser extent to watching other penguins being handled/ weighed (Regel & Pütz 1997).

With respect to **salt secretion**, Ainley (1974) found that salt secretion stopped during handling and was followed by hypersecretion after handling. In response to human visitation, hypersecretion occurred during-visit and continued for several minutes post-visit.

Comparing human disturbance to that of natural stressors, Ainley (1974) observed that in Adélie penguins hypersecretion occurred during, e.g., territorial defence, but did not persist after the conspecific encounter was concluded.

Increased stress-induced corticosterone levels have been examined in Magellanic (Fowler 1999; Walker & al. 2005; Walker & al. 2006) and Yellow-eyed penguins (Ellenberg & al. 2007). Fowler (1999) reported a reduced hormonal stress response with no significant difference between samples taken at capture (‘baseline’) and those taken 5 min later (‘stress-induced’) in Magellanic penguins ‘accustomed’ to human visitation (tourist area birds) as compared to birds sampled in an area restricted to scientific investigations or to birds from an ‘isolated’ area. Additionally, he found reduced within-group variability in corticosterone stress response in tourist area birds. In contrast, chicks from the same tourist area (Walker & al. 2005) were described to exhibit a higher corticosterone stress response than chicks from the other areas directly after hatching, but differences were no longer significant at 40-50 days post-hatching. A further paper from the same location (Walker & al. 2006) reported a 'physiological habituation' of plasma corticosterone levels to occur with regular exposure to human visitation, with tourist area penguins exhibiting a decreased capability of the adrenocortical tissue to secrete corticosterone. With respect to Yellow-eyed penguins, Ellenberg & al. (2007) found higher stress-induced corticosterone levels in penguins breeding at a location subjected to unregulated tourism (unsupervised, and unpredictable with respect to numbers of people present) as compared to those breeding in an area exposed to little visitation.

2.3.2.1.3 Concepts of Assessment of Disturbance: People as Predation-Free Predators?

A promising approach to investigating and assessing human disturbance has come from the field of **antipredator research** (Frid & Dill 2002; Ydenberg & Dill 1986). Comparison of animal responses towards human disturbance with those towards 'real' predators indicated that from the animals' point of view the two warrant similar reactions (e.g., Pépin & al. 1996, Beale & Monaghan 2004a). Culik & al. (1990a, p. 177) state that "[a] considerable increase in heart rate in otherwise undisturbed birds may result from the approach of a potential predator". In continuation, they refer to Ball & Amlaner (1980), who believed that these 'emotional' heart rate responses were adaptively significant and that they provided information on the bird's assessment of the danger to which it was exposed during approach. With respect to responses to humans, Neebe & Hüppop (1994), for instance, review a number of publications that report birds and mammals to react less intensely to humans or human objects (e.g., boats) moving parallel to them (i.e., tangentially passing by) as compared to directly approaching (i.e., coming towards) them, and suggest that birds correctly assess the direction of movement of a potential predator.

Ydenberg & Dill (1986) developed an **economic model of antipredator behaviour**. Emphasising that reactions towards potential predators involved the two-step process of 'detection' (knowledge/ awareness of the predator's presence) and 'response' (decision to act upon this knowledge/ awareness), they used fitness considerations (the trade-off between the costs of fleeing and the risk of remaining) to predict which actions should take place when. Within the framework of anti-predator research, human disturbance is thus assessed by examining the effects of different aspects such as approach type, conduct (behaviour of humans), distance, etc. Ydenberg & Dill's (1986) general model made the prediction that flight distance should increase with increasing cost of remaining (i.e., risk of capture) and decrease with increasing costs of flight. In the model, the relative costs of fleeing and staying thus change as the predator approaches. Their model was later modified by Blumstein (2003), who suggested that species have two critical distances (termed D_{min} and D_{max}, resp.) which create three discrete zones. Zone I constituted the area within which an animal would always respond to a detected threat; this zone was delimited by D_{min}, the minimum critical distance. Zone III, in contrast, lay beyond D_{max}, the maximum critical distance, i.e., the distance beyond which animals would no longer respond to a predatory stimulus. Ydenberg & Dill's (1986) original model comprised the area of zone II, in which the animals' risk assessment resulted in dynamic escape behaviour as a function of the perceived benefits and costs of flight.

For this study fleeing was outside the scope of the acceptable, as nest abandonment would expose the eggs to either predation by skua or death by freezing. Therefore, a more sensitive measure was chosen, viz., **'alert distance'**.

In terms of the model described above, alert distance marks the point in space and time at which the threshold of D_{max} has been undercut (awareness), and ingression into zone II has proceeded to that extent that an animal orients towards the disturbance (within the 'decision-making process' of whether to act upon awareness). While not being as 'costly' as flight, increases in vigilance behaviour also restrict the animal's opportunity to engage in other behaviours such as resting, nest maintenance or comfort, and may result in non-negligible extra energy expenditure (e.g., REGEL & PÜTZ 1997).

YDENBERG & DILL (1986) further suggested that neurophysiological responses, such as alterations in **heart rate**, could be used to examine whether an animal was aware of a given predator before behavioural flight responses occurred. Moreover, several penguin authors (for Adélie penguins, e.g., CULIK & WILSON, R.P. 1991, GIESE 1998) had even reported heart rate responses to occur *prior to any behavioural alteration* (i.e., not just well before flight occurred). In THIS THESIS, their findings have been incorporated (s.a., examination of 'parallelity or complementarity' of heart rate and behavioural indicators).

Table 2-7: Overview of Studies on Penguin Responses to Human Disturbance: Parameters and Methods of Measurement. Adélie penguin studies are presented first (a), followed by those on the remaining two pygoscelids (b) and other genera (c, d). Within species, studies have been sorted in reverse chronological order. For each study, parameters used and measurement methods employed are listed. For a brief summary of results, see text; the complete table is found in appendix 2-2.

Table 2-7 a) Adélie penguins (*Pygoscelis adeliae*) (page 1 of 2)

Species	**Species (lat.)**	**Disturbance Stimulus Examined**	**Behavioural Parameters [method of recording]**	**Physiological Parameters [method of recording]**	**Fitness Parameters**	**Author(s) (grey = abstract)**	**Year**	**Human impact found/ concluded**
Adélie	*Pygoscelis adeliae*	high level of human disturbance (station activities & tourists) vs. low level of human disturbance	none employed	none employed	numbers of breeding pairs; numbers of chicks in crèches; fledging success	Carlini & al.	2007	no
		station construction, airstrip construction, ongoing station activity	none employed	none employed	numbers of breeding pairs; breeding success (numbers of chicks fledged per pair)	Micol & Jouventin	2001	no
		human approach (1 person)	posture; agonistic acts (sideways stare alternate stare, point, gape, charge); vigilance (head turns); comfort; wing-flaps; headshakes; responses to conspecifics and skuas; recovery time of behaviour [video tapes]	heart rate [safety-pin electrode ECG; artificial egg, FM transmitter]	none employed	Giese	1998	yes
		scientific nest check (2 persons) vs. recreational visit (2 persons)	none employed	none employed	hatching success; chick survival	Giese	1996	yes
		tourist groups	none employed	none employed	chicks in crèches; chicks per pair	Patterson & al.	1996	no
		tourists; scientific activity	none employed [video camera suggested for future research]	none employed	breeding pairs; reproductive success	Acero & Aguirre	1994	yes
		human visitation	shifts of nest site location within colonies; pattern of colony distribution [notes]	none employed	breeding pairs; fledging success; within- and between-colony location (shifts)	Woehler & al.	1994	yes
		human presence; aircraft	deviation from normally walked routes [hourly counts for 10 min]; panic and flight behaviour [video tapes; time lapse]	heart rate [implanted heart beat frequency transmitters and detection electrodes, recordings by radio]	number of birds in colony; mortality rate	Wilson, R.P & al.	1991	yes
		sheathbill, congener, human helicopter, handling	rest, rest with head movement; standing still, standing & activity; disturbance behaviour incl. nest desertion [for chicks: oral notes on same tape as heart rate signal; stereo separation]	heart rate [safety-pin electrode ECG for adult birds; implantable radio transmitters for chicks]	breeding success (hatching of eggs)	Culik & al.	1990a	yes

Table 2-7 a) Adélie penguins (*Pygoscelis adeliae*) (page 2 of 2)

Species	**Species (lat.)**	**Disturbance Stimulus Examined**	**Behavioural Parameters [method of recording]**	**Physiological Parameters [method of recording]**	**Fitness Parameters**	**Author(s) (grey = abstract)**	**Year**	**Human impact found/ concluded**
Adélie	*Pygoscelis adeliae*	various disruptive (human) activities (helicopters, vehicles, noise, frequent foot traffic, scientific investigations); gradient of disturbance	none employed	none employed	breeding pairs	WILSON, K.-J. & al.	1990	yes
		field station related human activity in sub-colony close to hut vs. a sub-colony far from hut	shifts of nest site location within sub-colonies; pattern of sub-colony distribution [notes]	none employed	absolute numbers of breeding pairs, numbers of breeding pairs as %of entire Northern Colony	YOUNG	1990	yes (colony) no (population)
		manipulation (tail-feather clipping); attachment of devices of differing weight and hydrodynamic properties	incidence of nest desertion; duration of foraging trips [notes]	none employed	predictions based on findings included in discussion	WILSON, R.P. & al.	1989	yes
		scientific investigations; helicopters	none employed	none employed	breeding pairs; presence of non-breeders	OELKE	1978	yes
		uncontrolled visitor activity vs. controlled visitor activity ("caretaker scheme"); helicopters	none employed	none employed	breeding pairs; presence of non-breeders	THOMSON	1977	yes
		human presence at different distances	all comfort behaviours; vigilance (alert distance); recovery time behaviour [notes]	salt secretion [observation of unhandled birds; experimental salt administration]	none employed	AINLEY	1974	yes
		investigator presence close by, tail lift on nest, brief handling to obtain rectal temperature and body weight, longer-time handling	none employed	body temperature [device in abdominal cavity]	none employed	BOYD & SLADEN	1971	yes

Table 2-7 b) Other *Pygoscelis* species (page 1 of 1)

Species	**Species (lat.)**	**Disturbance Stimulus Examined**	**Behavioural Parameters [method of recording]**	**Physiological Parameters [method of recording]**	**Fitness Parameters**	**Author(s) (grey = abstract)**	**Year**	**Human impact found/ concluded**
Gentoo	*Pygoscelis papua*	human approach (1 person)	rest, head turns (vigilance); agonistics (defensive: threat-display, incl. low to high display; low threat to tête-à-tête; offensive: reaching or striking at offender); self-maintenance, chick-maintenance, comfort, bill-shakes; movement; recovery time of behaviour [notes]	none employed	mean number of crèche age chicks raised per pair	1. Holmes and (same dataset) 2. Holmes & al.	1. 2007 2. 2007/ 2008	yes
		human approach (1 person) on-station vs. human approach (1 person) off-station	rest; head turns (vigilance); agonistics (defensive: threat-display, incl. low to high display; low threat to tête-à-tête; offensive: reaching or striking at offender), self-maintenance, chick-maintenance, comfort, bill-shakes; movement; recovery time of behaviour [notes]	none employed	mean number of crèche age chicks raised per pair	Holmes & al.	2005/ 2006	yes (behaviour) no (fitness)
		human approach (1 person versus 5 persons)	vigilance activity; recovery time of behaviour [notes]	none employed	none employed	Holmes	2004	yes
		tourists-visited vs. non-tourist-visited colonies	none employed	none employed	number of breeding pairs; clutch size; hatching success; brood size; number of chicks in crèches; chick mass; number of chicks fledged per pair	Cobley & Shears	1999	no
		human approach (1 person, small groups, large groups); conspecifics; skuas	at rest; alert; low/ high threat, comfort/ stand and comfort; stand and social; stand and flee [video tapes; notes]	heart rate [artificial egg, infrared-sensor, cable]	total number of breeding pairs; total number of chicks in crèches	Nimon	1997	behaviour/ heart rate: only careless visitors; fitness: no
Chinstrap	*Pygoscelis antarctica*	human approach (1 person; indirect and slow vs. direct and fast)	distance when penguin first reacted; flight distance until stopping; escape angle; speed of flight [notes]	none employed	none employed	Martín & al.	2004	yes
		hand of intruding human (20 cm from penguin)	number of pecks given to intruder's hand within 10 s [notes]	none employed	clutch size; brood size	Viñuela & al.	1995	yes
		low-, medium- and high-impact human disturbance (decreasing distance from station incl. touristic activities)	none employed	none employed	breeding pairs; reproductive success	Acero & Aguirre	1994	yes

Table 2-7 c) ***Aptenodytes*** **and** ***Eudyptula*** **species** (page 1 of 1)

Species	**Species (lat.)**	**Disturbance Stimulus Examined**	**Behavioural Parameters [method of recording]**	**Physiological Parameters [method of recording]**	**Fitness Parameters**	**Author(s) (grey = abstract)**	**Year**	**Human impact found/ concluded**
Emperor	*Aptenodytes forsteri*	human presence (different numbers of people; range: 2-60 persons)	behaviour of the lead penguins of groups of travelling penguins (response distance, tolerance distance, avoidance) [notes]	none employed	none employed	BURGER & GOCHFELD	2007	yes
		station construction, airstrip construction, ongoing station activity	none employed	none employed	numbers of breeding pairs; breeding success (numbers of chicks fledged per pair)	MICOL & JOUVENTIN	2001	no
		weighing, feeding, stomach-flushing, ‘routine work’ in base camp, helicopter operations, 1 tourist visit	none employed	stomach temperature; recovery time physiology [ingested temperature loggers]	outlined by calculating energy expenditure and stress metabolic rates	REGEL & PÜTZ	1997	yes
Emperor chicks		helicopter approach and overflight	vigilance; wing-flaps; preening, comfort; posture; movement; recovery time of behaviour [video]	none employed	none employed	GIESE & RIDDLE	1999	yes
		prolonged handling	none employed	internal temperature; recovery time physiology [temperature loggers in abdominal cavity]	none employed	BOYD & SLADEN	1971	yes
King	*Aptenodytes patagonicus*	human approach (1 person)	rest; head turns (vigilance); defensive agonistics (bowing, ecstatic display; horizontal head circling), offensive agonistics (reaching or striking at offender); self-maintenance, chick-maintenance, comfort, bill-shakes; movement; recovery time of behaviour [notes]	none employed	none employed	1. HOLMES AND (same dataset) 2. HOLMES & al.	1. 2007 2. 2007/ 2008	yes
Little Blue	*Eudyptula minor*	unregulated tourism	none employed	none employed	nest numbers; penguins present (breeders and non-breeders)	GILING & al.	2008	yes

Table 2-7 d) *Eudyptes* species (page 1 of 1)

Species	**Species (lat.)**	**Disturbance Stimulus Examined**	**Behavioural Parameters [method of recording]**	**Physiological Parameters [method of recording]**	**Fitness Parameters**	**Author(s) (grey = abstract)**	**Year**	**Human impact found/ concluded**
Royal	*Eudyptes schlegeli*	human approach (1 person)	rest; head turns (vigilance); defensive agonistics (bowing to head-swinging), offensive agonistics (reaching or striking at offender); self-maintenance, chick-maintenance, comfort, bill-shakes; movement; recovery time of behaviour [notes]	see Holmes (2005)	none employed	1. Holmes and (same dataset) 2. Holmes & al.	1. 2007 2. 2007/ 2008	yes
		human approach (1 person)	resting (incl. comfort, excl. preening); maintenance (nest, egg, preening); posture; vigilance; agonistic; headshakes; swallows; wing movements [notes]	heart rate [artificial egg, FM transmitter]	none employed	Holmes & al.	2005	yes
		investigator disturbance (2 persons) at nest (direct approach) vs. at nests 3 m away from focal nests (tangentially passing by)	flight initiation distance mentioned [notes?]	none employed	number of active nests up to crèche stage	Hull & Wilson	1996	no
Rockhopper	*E. chrysocome*	investigator disturbance (2 persons) at nest (direct approach) vs. at nests 3 m away from focal nests (tangentially passing by)	flight initiation distance mentioned [notes?]	none employed	number of active nests up to crèche stage	Hull & Wilson	1996	no
Erect-crested	*E. sclateri*	no study found						
Fiordland crested	*E. pachy-rhynchus*	no study found						
Snares crested	*E. robustus*	human approach to colony edge, human approach within colony	not provided in abstract	heart rate [assumed: artificial eggs (cf. Ellenberg & al. 2006 for Humboldt penguins)]	reproductive success	Ellenberg & al.	2004	no

Table 2-7 e) *Megadyptes* and *Spheniscus* species (page 1 of 2)

Species	**Species (lat.)**	**Disturbance Stimulus Examined**	**Behavioural Parameters [method of recording]**	**Physiological Parameters [method of recording]**	**Fitness Parameters**	**Author(s) (grey = abstract)**	**Year**	**Human impact found/ concluded**
Yellow-eyed	*Megadyptes antipodes*	unregulated tourism vs. little visitation (scientific monitoring)	classification of four penguin personalities: aggressive, normal, calm, timid [notes]	corticosterone levels [blood sampling]	chick mass; fledging success	Ellenberg & al.	2007	yes
		unregulated tourism of varying intensity (numbers of tourists)	none employed	none employed	fledging weight; juvenile survival (extrapolated)	McClung & al.	2004	yes
		regulated tourism	chick-feeding patterns [notes]	none employed	nest numbers; fledging success	Ratz & Thompson	1999	no
Humboldt	*Spheniscus humbodti*	human approach (1 person) and presence	posture; nest/ egg manipulation; alternate stares; recovery time of behaviour [video tapes]	heart rate [artificial egg, microphone, cable]	breeding success (chicks fledged per pair)	Ellenberg & al.	2006	yes
African	*Spheniscus demersus*	human approach (3 persons)	vigilance; agonism; shifting position on nest; nest abandonment [notes]	none employed	none employed	Giese & al.	unpubl. data	yes
		human approach (1 person)	none employed	heart rate [artificial egg, FM transmitter]	none employed	DeVilliers & al.	unpubl. data	yes
		gradual approach (with intermittent pauses) vs. direct approach (without pauses) by 1 person	resting; walking; bathing; preening; "agitated behaviour"; distance at which 1st bird moved; distance at which approx. 50 % of the birds moved; distance at which approx. 75 % of the birds moved [notes]	none employed	presence of non-breeders (juveniles, moulting birds)	vanHeezik & Seddon	1990	yes
		at high-density colonies: 1-person gradual approach (with intermittent pauses) vs. 1-person direct approach (without pauses); at low-density colonies: 1-person walking through colony with differing intervals in-between successive passages	incubating; preening; "agitated behaviour"; posture (stand at nest, stand away from nest, lying down); exodus = mass departure [notes]	none employed	presence of non-breeders (prospecting birds)	Hockey & Hallinan	1981	yes

Table 2-7 e) *Megadyptes* and *Spheniscus* species (page 2 of 2)

Species	**Species (lat.)**	**Disturbance Stimulus Examined**	**Behavioural Parameters [method of recording]**	**Physiological Parameters [method of recording]**	**Fitness Parameters**	**Author(s) (grey = abstract)**	**Year**	**Human impact found/ concluded**
Magellanic	*Spheniscus magellanicus*	capture/ restraint vs. visits; human approach in tourist-area vs. human approach in non-touristically used area	defensive headturns (alternate stares) [notes]	corticosterone levels [blood sampling]	none employed	Walker & al.	2006	yes (corticosterone), but quick 'habituation'
		visits (1 person) at colonies frequently visited by tourists vs. unused to tourism, both during incubation and guard stage	vigilance; calls; posture; alert distance; flight initiation distance; severity of reaction assessed according to graded behavioural stress response (Yorio & Boersma 1992): 1. indifference; 2. head waving; 3. agitation; 4. abandon nest [notes]	none employed	number of breeding pairs; hatching success; fledging success	Cevasco & al.	2001	yes
		approach (1 person) in 3 areas differing in previous visitor exposure	offensive agonistics, defensive agonistics (alternate stares); rest; vocalisation; nest abandonment [notes]	corticosterone levels [blood sampling]	none employed	Fowler	1999	yes
		human approach in tourist area vs. non-touristically used area	threat and defensive displays; nest abandonment [notes]	none employed	breeding success; fledgling weights	Yorio & Boersma	1992	no
Magellanic chicks		approach until flight; restraint and capture in tourist-area vs. in non-touristically used area	avoidance distance; flight initiation distance [notes]	corticosterone levels [blood sampling]	chick mass	Walker & al.	2005	yes (corticosterone), but quick 'habituation'; no (chick mass)

2.3.3 Human Disturbance Assessment in the Field – Complementary Strengths of Behavioural and Heart Rate Parameters

> "[T]here is no single optimal method to quantify anthropogenic stressors." (Tarlow & Blumstein 2006/ 2007, p. 429)

Field studies encounter a number of problems which are absent or at least more easily soluble in laboratory (e.g., rodents) or on-farm (e.g., domestic ungulates) surroundings. Field conditions usually prevent subjecting animals to the majority of the tests commonly used on farms or in laboratories. Nevertheless, for non-invasive, hands-off field studies, **behaviour reactions** are well within the scope and are able to give what Dawkins (2003, p. 385) calls 'valence' to "physiological measures that might otherwise be ambiguous". Ambiguity may arise, for example, when due to lack of situational information, physiological excitation (e.g., increased heart rate) cannot be conclusively attributed to 'positive' (e.g., a returning mate) or 'negative' (e.g., an approaching predator) events. Behaviour is generally assumed to be the **most accessible of disturbance indicators** (e.g., see minimum approach distances, tab. 2-3 a) to c)), though this may be considered a mixed blessing, for instance, when untrained observers (e.g., tourists, non-penguinologists) fail to detect or correctly interpret biologically meaningful behaviour changes.

Heart rate, on the other hand, has often been proposed as being **more sensitive to disturbance than** (broad categories of) **behaviour**; and a number of studies report heart rate changes occurring without overt alterations in the behaviour of some or all of the animals studied in some or all of the disturbance situations examined (e.g., Culik & al. 1989 for Adélie penguins; Ellenberg & al. 2006 for Humboldt penguins; Ely & al. 1999 for Greater white-fronted geese, *Anser albifrons*; Neebe & Hüppop 1994 for Arctic terns, *Sterna paradisaea*). Moreover, cardiac response has later been identified as the best physiological measure for precisely quantifying stressors (Tarlow & Blumstein 2006/ 2007) in the field.

As outlined above, behaviour as well as heart rate responses have been used in **penguin studies** by a number of authors (tab. 2-7 s.a.) to assess reactions to disturbance stimuli. Despite the endeavours of many scientists, however, findings have remained controversial (for behavioural and physiological parameters, also see review above).

Summing up results for **Adélie penguins**, the majority of authors documented human impact on behaviour (Acero & Aguirre 1994; Ainley 1974; Culik & al. 1990a; Giese 1998; Wilson, R.P. & al. 1989, 1991), physiological (Boyd & Sladen 1971; Culik & al. 1990a; Giese 1998; Wilson, R.P. & al. 1991) and fitness parameters (Giese 1996 for smaller, though not for larger, colonies; Oelke 1978; Thomson 1977; Wilson, K.-J. & al. 1990; Woehler & al. 1994; Young 1990 on the colony, though not on the population, level), while other studies (behaviour and physiology not examined) reported no fitness or long-term effects (Carlini & al. 2007; Micol & Jouventin 2001; Patterson & al. 1996). A similar controversy generally arises with respect to the **other penguin species**. To a large extent this would seem attributable to the limits of comparability as regards studies in different geographical locations at different times during the breeding cycle, on different age or status groups[78], in colonies with different histories of human and other predatory (e.g., skua) exposure, conducted by different authors using different[79] (disturbance) indicators. In conclusion, site- and species-specific studies

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[78] age groups: adults, immatures/ juveniles, chicks; status groups: established breeders, unestablished breeders, non-breeders

[79] This is not a quote from Eggleton & Siegfried (1979); but see chapter 6.

are needed to assess the effects of human disturbance for particular penguins at particular times, and THIS THESIS aims at contributing to this task.

Employment of **behavioural parameters in conjunction with a physiological parameter** permitted

- context-specific interpretation of heart rate changes,
- determination of different sensitivities of the parameters towards human disturbance,
- investigation of individual coping strategies favouring either behavioural or physiological responses, and (as mentioned above)
- examination of parallelity or complementarity of behavioural parameters and heart rate.

2.3.4 Disturbance-Related Definitions

Comparable to other abstract concepts regularly used in every-day language (e.g., friendship, WASILEWSKI 2003), the term ‘human disturbance’ has been employed in penguin studies to denote a variety of human acts or actions (a general overview up to the mid-90s is found in NIMON & STONEHOUSE 1995; up to 2007 in DEVILLIERS 2008; also s.a., tab. 2-7). Examples include habitat destruction (by research station, road, or airstrip construction), direct bodily harm (killing or injuring adult penguins, destroying eggs or chicks), and various types of ‘psychologically repellent’, fear- or flight-inducing activities (actively/ advertently or passively/ inadvertently scaring penguins). Measurement as well as assessment of the effects of human disturbance has likewise been undertaken on different ‘levels’ (fitness effects on the population or colony/ rookery level; behaviour and physiological effects on the individual or group level). In conjunction, these facts account for some of the disparity in findings reported.

Human Disturbance

The **definition of human disturbance** used in THIS THESIS follows that proposed by NISBET (2000, p. 313):

> “Human disturbance is any human activity[80] that changes the contemporaneous[81] behavio[u]r or physiology of one or more individuals […].”

A number of issues concerning NISBET’s (2000) definition, however, need to be clarified prior to using it in the context of THIS THESIS. According to NISBET’s interpretation, disturbance need not necessarily have adverse effects. Some years earlier, ZEHNTER & SCHNIDRIG-PETRIG (1994) have pointed out that such a “neutral methodological approach” (ibid., p. 8: “Die ‘Neutralität’ des methodologischen Ansatzes…”), i.e., one that is initially ‘value-free’ and thus dependent on post-hoc discrimination between adverse, neutral, and beneficial effects, runs the risk of confusing matters[82] as it allows intuitively nonsensical combinations (e.g., adverse effects without disturbance; beneficial effects in the face of disturbance).

Moreover, NISBET (2000, p. 313) explicitly states that his wording defines “‘[d]isturbance as human activity, not as the response of birds to this activity”. As per his definition, however, classification of any human activity as constituting a disturbance precisely depends on the birds’ reactions, viz.,

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[80] excluding habitat destruction

[81] contemporaneous: (living or) occurring at the same time (WEBSTER 2003)

[82] not dissimilar to stress having been divided by some authors into ‘eu-stress’ and ‘dis-stress’ (see BROOM & JOHNSON 2000 for a comprehensive discussion)

changes in “the contemporaneous behavior or physiology” (ibid., p. 313). In this respect, Nisbet (2000, p. 313) points out that while it is the birds’ reaction which permits an activity to be classified as a disturbance (i.e., separating it from activities not eliciting a reaction), “the important issues are the nature and the magnitude of the effects and whether they are significantly adverse”. To further complicate matters, Nisbet’s definition and thus measurement of disturbance is based on individuals (“one or more individuals within a breeding colony”, ibid., p. 313), while the effects he suggests to accept as ‘adverse’ are on the population level.

A number of positive aspects of Nisbet’s (2000) definition have nevertheless led to its adoption within this thesis. As far as could be determined, he correctly pointed out (ibid., p. 313) that “the term ‘disturbance’ has not been defined in any of the prior reviews”[83] . Unlike the ‘binary distinctions’ of other reviews (e.g., Carney & Sydeman 1999: scientific investigators vs. tourists), Nisbet’s definition is eminently useful in bridging the gap between these different stressors by focusing on the activity performed rather than on the performer. Furthermore, the definition itself is explicitly based on individual birds and includes behavioural as well as physiological responses. Last, but not least, in measuring changes in the “contemporaneous behavior [sic] or physiology” (ibid., p. 313), it implicitly emphasises the necessity to determine an animal’s range of ‘normal’ behaviour and physiology prior to assessment of disturbance (e.g., Bateson 1991; Broom & Johnson 2000; Mayer 2007).

Given the nature and scope of this thesis, Nisbet’s definition is used strictly within the context of individuals, even when focal groups are examined: In this context, the state of welfare of the individual(s) will be focused upon, while the magnitude of adversity at the population level remains unextrapolated.

Human-Induced Disturbance Stimulus

In accordance with this definition, a human-induced disturbance stimulus was **defined** as the presence of human(s) – including the actions and/ or sounds emanating from that presence – that caused the animal(s) to deviate from their contemporaneous behaviour or physiology. The term ‘human-induced’ also accommodated the extremely rarely encountered instances of aircraft noise (not quantitatively evaluated).

Conspecific Disturbance

As for conspecific disturbance, the same **definition** applied, and the “contemporaneous behaviour/ physiology” of the animal(s) examined was compared between (intrusive) presence and absence of conspecifics.

Predator Disturbance

With respect to predator disturbance, the **definition** outlined for humans was employed. For this disturbance stimulus, only qualitative results are presented, as scarcity of observed interactions in this study did not permit quantification or comparative analyses (e.g., intensity of responses to humans vs. skuas).

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[83] Some of the early original papers, however, did offer quite succinct definitions, e.g., Ainley (1974, p. 17): “The effect of disturbance (human observer) on frequency of performance of seven comfort movements was assessed by recording the rate of performance while I (the disturbance) varied my distance from breeding colonies. Thus I was equating intensity of disturbance to the distance I stood from the birds.”

Stress and Stressor

As briefly mentioned above (section 2.3.1.1) the term **stress** is **defined** neither on an endocrinological nor on a fitness basis but used as a term descriptive of immediate behavioural and/or heart rate responses of the focal animal(s), comparable to SLADEN's (1958, p. 3) 'nervous strain'. In accordance with this, the term **stressor** is employed to connote the respective agent or activity perceived as the cause of the stress experienced by the focal animal(s).

2.4 Aims and Hypotheses

As outlined in the introduction, the **broad objective** of THIS THESIS was to comprehensively examine and evaluate the impact of human visitation on incubating penguins' behaviour and heart rate. Comprehensiveness was pursued by investigating impact on several aspects of penguin behaviour/ heart rate and by using different foci.

The ***foci*** employed serve to highlight different levels of penguin life (groups vs. individuals, within individuals: behaviour elements vs. behaviour systems):

Focal-group analyses using **broad behaviour categories** are performed to see whether this rather crude method of examination might already yield sufficiently clear results (particularly with respect to indicative behaviours and/or threshold distances) – results, which might be easily incorporated into codes of conduct for people visiting or working in the Antarctic.

Focal-animal analyses using a wide array of **behaviour elements** as well as **heart rate** are undertaken to gain an insight into individuality/ generality of responses. These are followed by focal-animal analyses focusing on **behaviour systems** and **heart rate patterns** – the **topography** of behaviour and heart rate. Here, two main points of interest are examined: 'systemic' shifts evoked by visitation and the extent of 'parallelity' or 'complementarity' of behavioural and physiological responses.

Overall, seven objectives (five of which concern 'fundamental' or 'pure' science; while the last two seek to contribute to applied science) are addressed:

Aims I and II: Starting with the objectives pertaining to 'pure science', THIS THESIS aims at examining the **strength of impact**, first in focal groups (FG: behaviour only), then in individual focal animals (FA: behaviour and heart rate) **on** penguin **behaviour** and **heart rate**.

Aim III: Extent of individuality of responses of focal animals (FA) is looked at to investigate the different coping strategies employed by individual focal animals and to thus determine whether for these penguins 'average responses' represent an adequate measure of the impact of disturbance.

Aim IV: Comparison of responses to human visitation with those to conspecific disturbance (FG, FA) is undertaken in the search of a means to 'ground' the extent of human impact to an 'everyday-', i.e., natural stressor and to gain insight into the 'relative importance' the penguins might attribute to either disturbing agent.

Aim V: Impact of different visiting regimes (FG, FA) is examined to identify key features alleviating/ enhancing impact (number of visitors/ visitor conduct). With respect to disturbance to breeding birds, the type of disturbance is assumed to be of greater relevance than the purpose (tourism, leisure, science) of the disturber[84] .

Aims VI and VII: Two ‘applied objectives’ complement these ‘pure science’ aims: The first is to find **indicative behaviours** that could be used to enable short-term or untrained observers (such as, e.g., tourists) to reliably identify their impact. The second is to determine robust **threshold distances** adherence to which would markedly reduce signs of disturbance.

Within the context of all seven aims, discriminatory capacities of different sampling and transcription methods will be compared as to their sensitivity concerning detection of changes in behaviour, posture and/or heart rate.

N.b.: While presentation of results mirrors the different foci, the catalogue of aims will be reflected in the structure of the discussion. Table 2-8 provides an overview of aims and hypotheses formulated. Please also note that the ‘applied aims’ did not receive any working hypotheses as they were considered ‘meta-aims’ the fulfilment of which would depend on results obtained for the ‘pure science’ aims.

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[84] While it is undoubtedly true that in terms of numbers of people, the danger of ‘the more the messier’ exists, it is beyond the scope of THIS THESIS to adequately analyse the cumulative impacts of the various factors determining avian perception of larger groups of humans (e.g., compactness vs. spreading out, cumulative noise levels, cohesive vs. widely disparate and/or dispersed movements, etc.). The discussion section, however, will try to broaden the scope to that effect.

Table 2-8: Aims and Hypotheses. Aims are distinguished by main areas of science results contribute to (pure vs. applied).

Aims – Pure Science	Hypotheses
Examine the Impact of Human Visitation on Incubating Penguins' Behaviour and Posture (=Behaviour s.l.)	**H_0: There will be no differences in behaviour s.l. before, during, and after human visitation.**
	H_{1A}: Behaviour s.l. during visitation will differ from behaviour s.l. before visitation.
	H_{1B}: Behaviour s.l. during visitation will differ from behaviour s.l. after visitation.
	H_{1C}: Behaviour s.l. after visitation will differ from behaviour s.l. before visitation.
Examine the Impact of Human Visitation on Incubating Penguins' Heart Rate	**H_0: There will be no differences in heart rate before, during, and after human visitation.**
	H_{1A}: Heart rate during visitation will differ from heart rate before visitation.
	H_{1B}: Heart rate during visitation will differ from heart rate after visitation.
	H_{1C}: Heart rate after visitation will differ from heart rate before visitation.
Examine the Extent of Individuality (Coping Strategies) re Response to Human Visitation	**H_0: There will be no inter-individual differences in penguin behaviour s.l. and/ or heart rate during disturbance.**
	H_1: Inter-individual differences in behaviour s.l. and/ or heart rate will be present during disturbance.
Compare the Impact of Human Visitation to that of Conspecific Disturbance	**H_0: There will be no differences in penguin responses to conspecific and human disturbance.**
	H_1: Penguins will respond differently to human than to conspecific disturbance.
Examine the Impact of Different Visiting Regimes (Visitor Conduct and Number)	**H_0: There will be no differences in penguin responses to different visiting regimes.**
	H_{1A}: Penguins will react more strongly/ less weakly to 'loud and fast' as compared to 'silent and slow' visitor(s).
	H_{1B}: Penguins will react more strongly/ less weakly to three visitors as compared to one visitor.
Aims – Applied Science	
Find Indicative Behaviours/ Postures	} Derived meta-aims: Fulfilment depends on results.
Find Threshold Distances	

3 Animals and Location

> "Penguins are one of the oldest, most aquatic, and arguably most mystifying groups of birds." (Kooyman 2002, p. 485)

N.b.: In order to place the study presented in this thesis into context, data are summarily provided on penguin colonies throughout the entire Adélie penguin breeding range. To facilitate detection of study site-specific information (SSSI 13/ ASPA 132, Potter Peninsula, 'Isla 25 de Mayo'/ King George Island, South Shetland Islands; 62°15'S, 58°39'W), the respective PLACE NAMES/ LOCALITIES are presented in underscored capitals.

3.1 The Adélie penguin, *Pygoscelis adeliae*[1]

3.1.1 Taxonomic Classification, Morphology and External Appearance

3.1.1.1 Taxonomic Classification

Order:	Sphenisciformes[2]
Family:	Spheniscidae
Genus:	*Pygoscelis*
Species:	***P. adeliae*** (Adélie penguin)
	P. papua (Gentoo penguin)
	P. antarctica (Chinstrap penguin)

> "The first fossil penguin to be described was found by an unnamed 'native', undoubtedly a Maori, near Kakanui, New Zealand, acquired by Dr. W.B.D. Mantell, forwarded by him to Thomas Henry Huxley, and published by the latter in 1859 as *Palaeodyptes antarcticus*[3]." (Simpson 1975, p. 20)

The origins of the **family Spheniscidae** are probably rooted in the Cretaceous period, i.e., 140-65 MYA[4] (Simpson 1976). The oldest fossil penguin so far discovered, however, is a much more recent specimen, consisting of a partial skeleton from late Palaeocene or early Eocene deposits (60-50 MYA), found at Waipara, near Canterbury in New Zealand by Ewan Fordyce and colleagues. A 10-15 million-year gap in the fossil record divides this specimen from penguin fossils of the late Eocene period. By this time, numerous distinct and already highly specialised penguin-like species appear to have evolved, many of which have been described by – as Williams (1995, p. 10) aptly puts it – "one of the doyens of penguin palaeontology", George Gaylord Simpson. Remains of fossil Spheniscidae have so far only been reported from localities in the southern hemisphere, and their distribution is very similar to that of modern-day species. It is now generally accepted that penguins evolved from a flying ancestor, perhaps similar to modern-day diving petrels (Pelecanoididae) or auks (Alcidae). (Williams 1995)

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[1] (Hombron & Jacquinot, 1841), Ann. Sci. Nat. Zool. Paris ser. 2, 16:320 – Adélie Land

[2] Despite Sibley & Ahlquist's (1990) attempts to lodge the penguins with the Ciconiiformes, more recent authors (e.g., Bertelli & Giannini 2005) retain the order Sphenisciformes in their classification.

[3] from rocks probably dating back to the Oligocene age (30-25 MYA)

[4] MYA = million years ago

There are **six genera** of extant penguins (*Aptenodytes*, *Pygoscelis*, *Eudyptes*, *Megadyptes*, *Spheniscus*, and *Eudyptula*) containing a total of **16 to 18 species**[5]. Among these, the largest species is the Emperor penguin (*Aptenodytes forsteri*; 30 to 38 kg, Reilly 1994; max. weight: 41 kg, Wilson, E.A. 1907, as quoted in Williams 1995; body length: 100 to 130 cm, i.e. standing height of almost a metre, Reilly 1994), who is twice the mass of their congener, the King penguin (*A. patagonicus*), and 30 times the mass of the smallest present-day penguin, the Little blue[6] penguin (*Eudyptula minor*; approx. 1 kg Reilly 1994; max. weight: 2130 g, Marchant & Higgins 1990; body length: 40 to 45 cm, Reilly 1994). Some of the fossil species, however, were probably substantially larger than the Emperor (Kooyman 2002).

Today[7], the **Adélie penguin** shares a genus with two other species, viz., the Gentoo (*P. papua*) and the Chinstrap penguins (*P. antarctica*). The generic name, *Pygoscelis*, is Greek for 'rump-legged'[8]; it was coined by the German naturalist Johann Wagler in 1832 (Ainley 2002). The Adélie's second name (*adeliae*) can be traced back to Adéle, wife of the French expedition leader Jules-Sébastien-César Dumont d'Urville. During his journey in the Southern Ocean (1837-40), which also took him and his crew around the Antarctic continent, Dumont d'Urville named a part of the Antarctic coast (Adélie Land, 66°33'S, 139°10'E) after his wife; and the Adélie penguin, in turn, received its name from this place, "where its breeding colonies were first visited by humans and critical scientific specimens were obtained" (Ainley 2002, p. 5).

3.1.1.2 Morphology and External Appearance

With a body **length** of 70 cm, the Adélie penguin is a medium-sized penguin, approximately midway between the Emperor penguin (*Aptenodytes forsteri*) and the Little blue penguin (*Eudyptula minor*). Its **weight** varies markedly throughout the season, with peak weights prior to moult[9] (6770 g, Penney 1967) and a substantial mass loss during the courtship period. At KING GEORGE ISLAND, Trivelpiece & Trivelpiece (1990) recorded a mean weight loss of approximately 1,000 g (SE: ±100 g) between arrival prior to breeding (5350 g) and departure after moult (4340 g) in 26 Adélie penguins.

Generally speaking, the Adélie penguin is the prototype of a black and white penguin (fig. 3-1). As described in Williams (1995, p. 169f.), adult Adélies exhibit a distinct **colouring** directly after the moult, the head, upperparts of the body, and tail are blue-black with the colour fading to brown in the course of a year. The head is marked by a distinctive ring of white feathers around the eye. The underparts (belly, legs) are pure white, and a sharp V-shaped demarcation separates them from the black chin and throat. Dorsally ('on the upper side/ outside'), the flippers are blue-black with a narrow white trailing edge; ventrally ('on the underside/ inside'), they are white with a thin blackish leading edge and a small dark area at the tip. The bill is mainly black with some orange-red at its base. It appears short because it is covered with feathers over half its length. The iris is brown, and the bright white sclerae are usually not seen unless the bird is agitated. Likewise, the black-feathered nasal, ocular and occipital crests are raised during expression of certain behaviours (e.g., agonistic, display, ruffle-shake), but are not seen if the birds are at rest. The legs and feet are dull white to pink, the soles are black.

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[5] Debates continue, whether certain differences ought to be granted species-status.

[6] also simply called Little penguin (e.g. by Warham 1958, Williams 1995)

[7] Jacques Hombron and Honoré Jacquinot originally named the Adélie penguin *Catarrhactes adeliae*, but in 1898, William Ogilvie-Grant of the British Museum of Natural History argued successfully for its inclusion in the genus *Pygoscelis* (Ainley 2002).

[8] pyg-: *πυγη* = *πυγαι·ον* = rump; scel-: *σκελ·οζ* = thigh, shin, leg, foot (Werner 1972)

[9] change of the complete set of feathers at the end of the breeding season

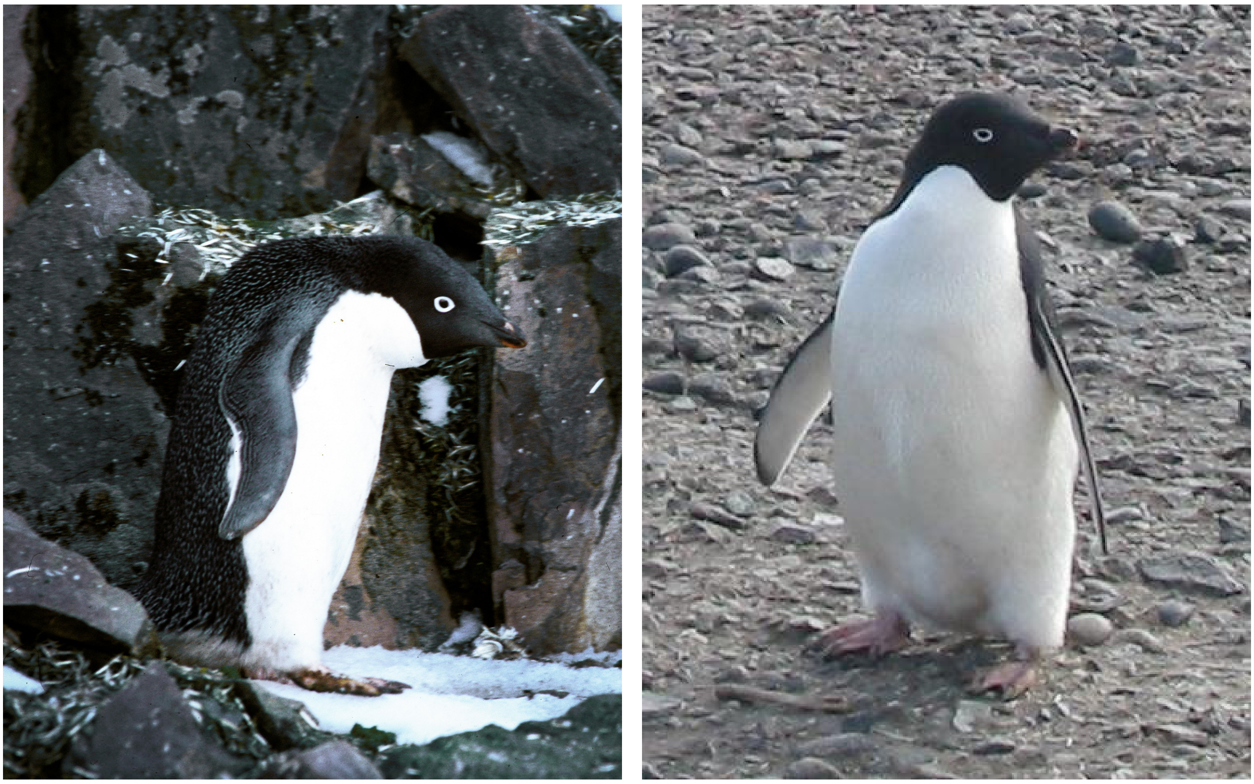

Figure 3-1: Adélie Penguin. The sexes are similar in appearance, and individual recognition is hampered by a distinct lack of distinguishing features – at least for the human sensory system. The dark face (cf. Chinstrap penguin: black cap, white face, and, of course, black chinstrap) which lacks head-markings (cf. Gentoo penguin: white 'telephone receiver' on top of head), and the lack of a coloured crest (cf. Crested penguins, *Eudyptes* spp.) and breast-bands (cf. *Spheniscus* spp.) separates adult Adélies from all other medium-sized penguins. © K.Schuster 2000

To the human eye, male and female Adélies are very similar in appearance throughout the year. In a review on sexual dimorphism in penguins, Agnew & Kerry (1995, quoting Kerry & al. 1992) state that even using discriminant analysis, success rates of only 85 % are achieved when attempting to determine the sex of Adélie penguins from morphological features. Although males have been found to be (statistically) significantly larger than females, reliable **sexing** requires the measuring of bills or employment of a method termed cloacal examination (only useful around egg-laying time, when the female's cloaca is wider than the male's). Furthermore, visual **recognition of individuals** is largely impossible without artificially marking the birds[10], for unlike some other penguin species (e.g., Yellow-eyed penguin, *Megadyptes antipodes*, penguins of the genus *Spheniscus*), Adélie penguins lack distinguishing natural marks (e.g., individual black feathers on the white breast; cf. African penguin recognition programme developed by Burkhardt & al. 2004).

3.1.2. Range and Status

3.1.2.1 Geographical Range

> "Adélie penguin colonies are not distributed evenly in Antarctica. Very few colonies exist in the vast stretches of ice cliffs that border the Weddell Sea. In contrast is the other great sea of Antarctica, the Ross Sea, on the opposite side of Antarctica. Along the Victoria Land coast, the western border of the Ross Sea, we find more than 744,000 nesting pairs of this species, or about 30 percent of the world's breeding population." (Ainley 2002, p. 88)

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[10] In this thesis, blue paint applied to several strategically valuable body regions served to distinguish between the two partners of a nest ('semi-individual').

The Adélie penguin's **range** is circumpolar (fig. 3-2) in that birds breed from Cape Royds (on the western corner of Ross Island; 77°S, 168°E) in the Ross Sea, along the coast of the Antarctic continent and the West coast of the Antarctic Peninsula, on the islands of the Scotia Arc, and 'northwards' up to the South Sandwich Islands (approx. 60°S, approx. 28°W) and Bouvetøya Island (54°S, 3°E). AINLEY (2002, p. 25f.) circumscribes the Adélie's pelagic (non-breeding) distribution by linking it to sea ice, in that "sea ice at its maximal extent defines the at-sea range of this species". The Adélie is vagrant to South America, Australia, New Zealand, and the sub-Antarctic islands in the Indian and Pacific Oceans (WILLIAMS 1995).

Like the majority of seabird species, the Adélie penguin is a colonial breeder (AINLEY 2002). The **breeding colonies** occur on rocky islands, peninsulas, beaches, scree slopes etc., wherever the land is ice-free and accessible from the sea. At high latitudes, the colonies are often found in areas exposed to the sun and wind so they remain free from snowdrifts (TENAZA 1971; MÜLLER-SCHWARZE & MÜLLER-SCHWARZE 1975, quoted in WILLIAMS 1995). At lower latitudes, more sheltered sites are

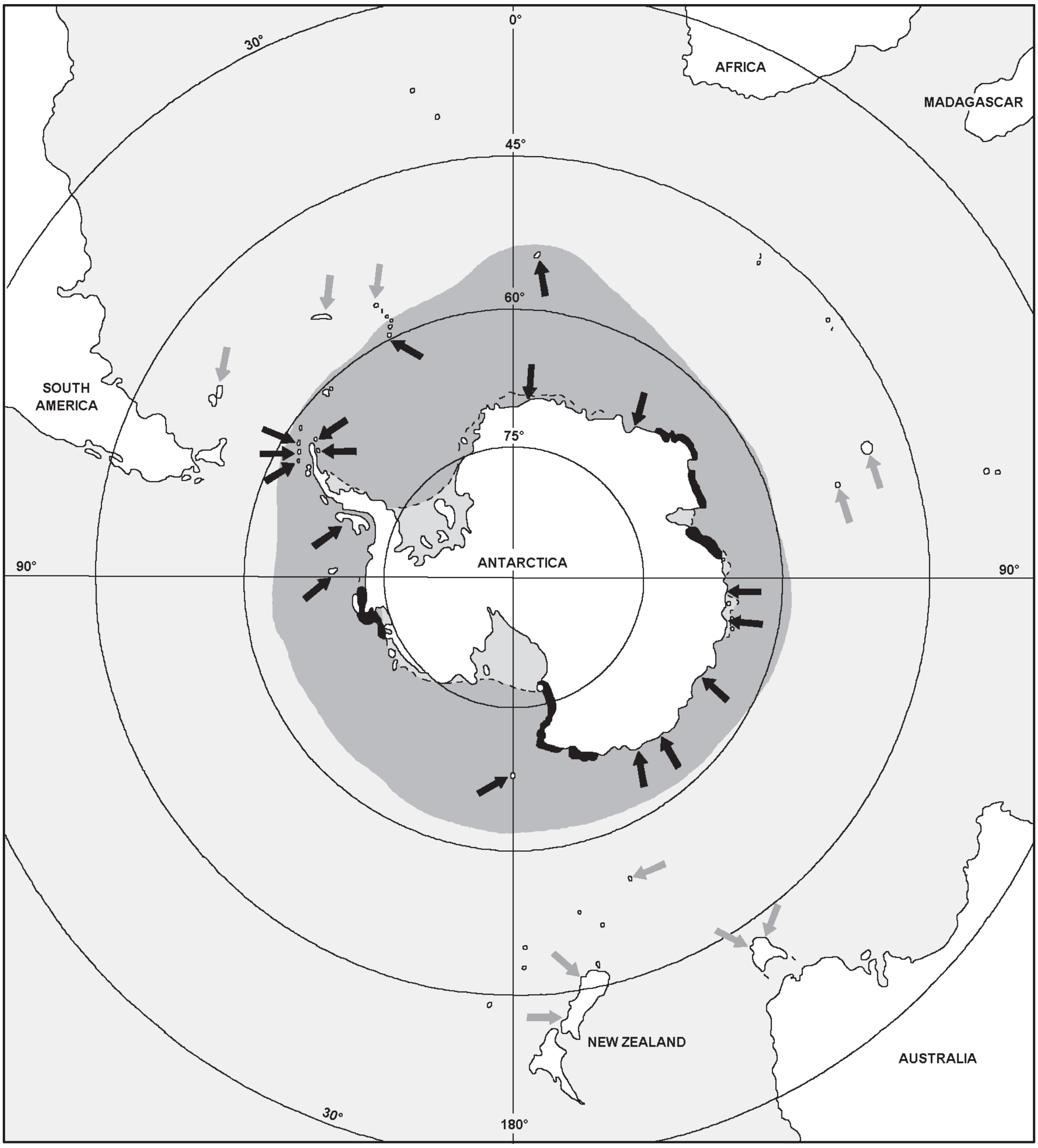

Figure 3-2: Range of Adélie Penguin Breeding Sites (black arrows) and Sightings of Vagrant Birds (grey arrows). Redrawn from WILLIAMS (1995).

preferred (Volkman & Trivelpiece 1981). The **size** of breeding colonies ranges from just a few to over 150,000 pairs. To some extent, the breeding range of the Adélie penguin overlaps with those of its congeners (i.e., Gentoo, *P. papua*; Chinstrap, *P. antarctica*), and many of the smallest 'Adélie colonies' (less than 100 pairs) actually constitute Adélie penguins breeding within larger colonies of Chinstrap or Gentoo penguins. At the study site used for this thesis, all three species bred in SSSI 13 (now ASPA 132; s.b.). While there was little or no mixing between the Gentoo and the Adélie nests, the Chinstrap breeding area was directly adjacent to an Adélie-only colony, and Adélie nests were found among the Chinstraps.

The **main breeding populations** are found in the Ross Sea region (744,000; see quote above), on the Antarctic Peninsula and the Scotia Arc (727,000), and Prydz Bay (395,000; Ainley 2002). The largest single colony was reported at Cape Adare, Victoria Land (71°18'S, 170°09'E), with an estimated 169,200[11] breeding pairs (SCAR 1996).

To date, the **total population** is estimated as at least 2,610,000 breeding pairs (Woehler 1993, as quoted in Woehler & Croxall 1997) and 10,000,000 immatures (Croxall 1985, as quoted in Williams 1995). According to Ainley (2002, p. 87), an estimate of Adélie penguin breeding pairs would vary between 2.4 and 3.2 million worldwide; with the vagueness of the figure owing to different estimation methods used by different researchers.

3.1.2.2 Conservation Status

In Williams (1995), the species' general **status** is described as being stable or increasing, and in 2004, the IUCN[12] Red List Category was given as **'Least Concern'**. Figures reported, however, vary among studies[13].

In the **Ross Sea**, Taylor & al. (1990, quoted in Williams 1995) found Adélie populations to have increased between 3 % and 30 % at all colonies (n = 38) from 1981 to 1988. Increases averaging 3.7 % per annum have been reported at Wilkes Land, **East Antarctica**, between 1963 and 1983, with new colonies growing by 11.7 % per annum (Martin & al. 1990, quoted in Williams 1995). According to SCAR[14] (1996), however, colonies have since then been on the decline again. Populations on the **Antarctic Peninsula and nearby islands** increased between the 1950s and late 1970s. More recently, populations have either fluctuated substantially but remained generally stable overall, or decreased locally (Penguin CAMP[15] Report, August 1998, as quoted in CBSG[16] Penguin Conservation Workshop, Ushuaia 2004). Numbers in the **AAT** (Australian Antarctic Territory, an area which holds about 27 % of the total population) appear to be stable or increasing (Woehler 1993).

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[11] N.b.: A previous count in the mid-1980s had reported 282,307 pairs (Taylor, Wilson & Thomas 1990).

[12] International Union for the Conservation of Nature and Natural Resources

[13] N.b.: While Oelke (1978, quoting Prévost 1976) reports numbers of Adélie penguins (regardless of reproductive status) to amount to approximately 27,000,000, more recent publications distinguish between breeders (reported as number of breeding pairs) and immatures, and come to a strikingly lower total (i.e., approx. 15,220,000 individuals). With respect to this discrepancy, Croxall (1984) criticised that a study co-authored by Prévost (Mougin & Prévost 1980, quoted in Croxall 1984) assessed the non-breeding population of penguins as over twice the breeding stock, which Croxall suggested (ibid., p. 597) to be "greatly at variance with information on penguin demography". It is assumed that the same bias aggrandised the figure quoted by Oelke (1978).

[14] Scientific Committee on Antarctic Research

[15] Conservation Assessment and Management Plan

[16] Conservation Breeding Specialist Group

With respect to KING GEORGE ISLAND, South Shetlands, where THIS STUDY was conducted, however, populations monitored at **Admiralty Bay** (location of SSSI 8, now ASPA 128) from 1976 to the present were highly variable but stable until the late 1980s, and then declined sharply. For this area, mean population counts “from 1990 to the present” are lower than mean counts “for 1976 to 1988” by 30 % (Penguin CAMP Report, August 1998, as quoted in CBSG Penguin Conservation Workshop, Ushuaia 2004) to 35 % (SCAR 2001).

As for **Potter Peninsula**, AGUIRRE (1995) reported 14,554 pairs of breeding Adélie penguins at STRANGER POINT (SSSI 13/ ASPA 132) whereas (personally witnessed) censuses in 2000 and 2001 yielded approximately 7,300 and 5,500 breeding pairs, respectively. This was confirmed by SANTOS & al. (2004), who reported a continuous decrease from 1998 to 2002, when the number of breeding pairs totalled only 49 % of those counted in 1995. Even though these figures might not be entirely compatible (the 2000/ 2001 censuses were effected by counting nests with eggs and nests occupied; the author of THIS THESIS does not recall census methods poster-presented by SANTOS & al. 2004), the general trend for this area appears to be a declining one.

The Adélie penguin has been **classified** as being **susceptible to human disturbance**, with local decreases in population size caused by the construction of research bases in the Ross Sea, at Cape Royds, and at Terre Adélie (= Adélie Land), though stricter regulations on human activity have resulted in the colonies’ returning to former numbers of breeding pairs (HARPER & al. 1984; JOUVENTIN & al. 1984; both quoted in WILLIAMS 1995). The Penguin CAMP Report (August 1998, as quoted in CBSG Penguin Conservation Workshop, Ushuaia 2004, p. 42) lists the following existing and potential threats to the Adélie penguin in the Antarctic Peninsula area (boldface added here):

a) the persistent, restricted location of commercial krill fishing in waters adjacent to breeding populations during their breeding season (AGNEW & PHEGAN 1995, as quoted in CBSG Penguin Conservation Workshop, Ushuaia 2004, p. 42),

b) oil pollution and other marine pollutants such as organochlorines,

c) **direct human disturbance, especially in the vicinity of stations (and particularly on KING GEORGE ISLAND) and at sites frequently visited by tourists**.

3.1.3 Breeding and Life Cycle

> “The annual cycle of an Adélie penguin includes a premigratory period of feeding and fattening, spring migration to the colony, nesting, fall migration from the colony, continued heavy feeding, and then molt[17] [sic]. All this takes about six to seven months; the remaining months – fall and winter – are ones of little activity.” (AINLEY 2002, p. 99)

The Adélie is migratory during the **non-reproductive phase** (May to August), but requires ‘terra firma’ for all the activities linked to raising offspring. Adult birds arrive at their colonies during September and October (date of first return, KING GEORGE ISLAND: 28 September-18 October; JABLONSKI 1987, quoted in WILLIAMS 1995). At KING GEORGE ISLAND, two studies did not detect a significant difference in date of **arrival** between the sexes (SPURR 1975c; TRIVELPIECE & TRIVELPIECE 1990), although males have been found to generally arrive earlier than females by up to four days. Date of arrival is related to latitude as well as sea-ice conditions in spring[18], being delayed in heavy ice years (AINLEY & LERESCHE 1973).

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[17] At lower latitudes, moult may precede fall migration, i.e., the birds moult in the breeding colony.

[18] N.b.: Month-wise, spring in the Southern hemisphere is roughly equivalent to autumn in the Northern one.

Table 3-1: Adélie Penguin Life Cycle. With respect to arrival until egg-laying, average number of days is given for KING GEORGE ISLAND (KGI) specifically. Extracted from WILLIAMS (1995).

Month	Activity	Average Number of Days
Sept./ Oct.	arrival till egg-laying	21 (KGI), may be shorter at other locations
Nov./ Dec.	incubation period till hatching	35-39 (1st eggs in 2-egg clutch); 33-38 (2nd eggs)
December	hatching till end of guard stage	18-27
January	crèche stage till fledging	30-43
Feb./ Mar	pre-moult feeding	highly variable: a few days to over a month
Mar./ April	moult till leave for sea	15-23
May-Sept	at sea (migratory stage)	remainder

At SSSI 13[19] (now ASPA 132[20]) (see maps in section 3.2), the largest sub-colony (in which the study presented here took place) is situated on an ‘elevated plain’, while the spatial pattern of small sub-colonies (fig. 3-23) reflected the area’s topography: the nests were concentrated on little mounds which lost their snow and ice cover more rapidly than their surroundings, and were thus accessible for nest building earlier than the lower plains around them. According to TRIVELPIECE & TRIVELPIECE (1990), **site-fidelity** on KING GEORGE ISLAND is high: 98.9 % (98.1-100, n = 4 years) of males and 65.5 % (61.8-72.9) of females returned to the same nest in successive seasons; and in 6 years less than 0.1 % of females and no males were found breeding at a colony different to that in the previous year. In general, AINLEY & al. (1983) reported that of those birds that survive to breeding age, 96 % breed at their natal colony, the remaining 4 % at an adjacent colony; 77 % of the birds they studied bred within 100 m of their natal site. Although the Adélie is typically monogamous (WILLIAMS 1995), **pair-fidelity** has been found to vary between seasons (e.g., KING GEORGE ISLAND: 62 % of birds retained the same mate between years); among other things, fidelity depends on synchronicity of arrival and interseasonal survival of both partners. Furthermore, a latitudinal variation has been observed:

> “The shortness of the breeding season and the consequent importance of arrival and breeding cycle synchrony are no doubt the reason why mate fidelity is low in Adélie penguins of the southern Ross Sea, compared with birds of lower latitudes and with other long-lived seabirds.” (AINLEY 2002, p. 146)

While the male selects the nesting site and initiates the nest-building, both partners contribute to completion and maintenance of the nest once pair formation has occurred. The **nest** consists of a shallow scrape surrounded by, and lined with, pebbles. These pebbles are a constant source of conflict between incubators and roaming conspecifics, as all the nests in a colony are continuously repaired and added to. Not infrequently, the pebbles added to one’s own nest are obtained from the nest of a momentarily inattentive neighbour (MORENO & al. 1995a, b; LEVICK 1914; SLADEN 1958). The mean **inter-nest distance** found on KING GEORGE ISLAND (43.2 ± 1.3 cm) is smaller than at other locations (e.g., 78-108 cm at Cape Crozier; WILLIAMS 1995). Generally speaking, Adélie territories within a colony are small and tightly packed. As AINLEY (2002, p. 74) puts it:

> “[T]erritories are contiguous. That is, the outer edge of one territory abuts the outer edge of at least one other territory. If it stretches full length, a penguin sitting on its nest can catch and lock its beak with that of its neighbor [sic]; also stretching full length from its nest.”

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[19] Site of Special Scientific Interest

[20] Antarctic Specially Protected Area

Once ashore, both birds remain at the nest until egg-laying (mean time between arrival and laying of first egg: 21 d for KING GEORGE ISLAND, tab. 3-1). As in other penguin species, **copulation** occurs many times during the pre-egg stage, but coition is often incomplete (MARCHANT & HIGGINS 1990) and may – especially in inexperienced breeders – lead to the deposition of infertile eggs. **Egg-laying** is highly synchronous, and 50 % of the clutches are initiated over a six-day period. Adélies usually lay two eggs, but a third egg may be 'added' as a substitute for a first egg if the latter is lost or removed within 24 hours of laying (ASTHEIMER & GRAU 1985, quoted in WILLIAMS 1995; TAYLOR 1962). If an entire clutch is lost, however, no replacement occurs, possibly because of the short breeding season (SLADEN 1958; TAYLOR 1962). Mean **clutch size** is further influenced by the age of the female (among three-year olds, a significantly greater proportion lay one-egg clutches), fat reserves (deduced from late laying date after unusually late arrival which indicated overly difficult migration caused by heavy sea ice conditions; AINLEY 2002) and relative location of the nest (SPURR 1975a, TENAZA 1971), with the proportion of two-egg clutches increasing from isolated to peripheral to central nests. Mean **egg size** at four locations (reported in WILLIAMS 1995) varied between 68.4 and 70.5 mm of length and between 54.2 and 56.2 mm of breadth. Mean **egg weight** ranged from 113.2 to 124 g. First eggs are significantly larger than second eggs (YEATES 1968). SPURR (1975c) found the **laying interval** between first and second egg to average 3.0 days. Full **incubation** does not begin until the second egg is laid, and a hatching interval of 1.4 days indicates an equivalent of only 34 h of (discontinuous) incubation during the three-day laying interval (TAYLOR 1962; SPURR 1975c). Both sexes incubate in alternate shifts, usually starting with the male[21], although reverse incubation patterns have been reported (e.g., TAYLOR 1962). The timing of the **change-overs** (nest relieves) may also vary; two long shifts and a third shift of medium-length (e.g., SLADEN 1958: 13, 15, 8 days; TAYLOR 1962: 11, 11, 8 days) followed by several short ones are most commonly observed, but the combination of two long shifts (16.6, 12.3 days) followed by several shorter ones is not unknown either (DAVIS 1982). Annual variation in shift length has been suggested to be linked to sea ice conditions (with shorter shifts observed in years of earlier break-up of sea ice, YEATES 1968) or food availability (AINLEY 2002). For KING GEORGE ISLAND, TRIVELPIECE & al. (1990) found the total number of shifts ranging from 3 to 7. The average **incubation period** lasts 35-39 d for first eggs and 33-38 d for second eggs (tab. 3-1). MÜLLER-SCHWARZE (1968) and DERKSEN (1977) suggested a circadian rhythm in some activities of Adélie penguins during incubation, while YEATES (1971, as quoted in DERKSEN 1977) found no such pattern. **Hatching** is typically asynchronous (eggs hatch on average 1.4 d apart within a clutch). Hatching success varies between years (e.g., DAVIS 1982b, egg losses due to nest desertion: 1st year of study = 27.5 %, 2nd year = 47.5 %) and localities. Addled or infertile eggs, nest desertion, and predation have been listed as causes for egg failure. After hatching, the chicks are guarded and brooded[22] continuously by one parent for 18 to 27 days. Change-overs during **guard stage** occur every day or twice in three days (TAYLOR 1962), and guard duties are shared roughly equally by males and females (spending 55 % and 45 % of the time guarding, respectively). Guard stage is followed by **crèche**[23] **stage**, during which the chicks aggregate in small groups (10-20 birds), while both parents leave the colony in search of food. The returning parent feeds the chicks; at KING GEORGE ISLAND, chicks were found to receive 0.99 feeds per day, with a mean feeding interval of 24.3 ± 0.8 hrs (TRIVELPIECE & al. 1987). Mean **age at fledging** ranges between 48.4 and 61.3 days (TAYLOR 1962; AINLEY & SCHLATTER 1972; LISHMAN 1985). Chick loss may occur through predation (particularly by Skuas, *Catharacta*

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[21] while the female replenishes body supplies after egg-laying

[22] Adélie chicks do not develop thermoregulation until about 10 to 15 days of age (GOLDSMITH & SLADEN 1961).

[23] A crèche is defined as three or more chicks closer to one another than half the inter-nest distance (AINLEY 2002). The term crèche is meant to imply simply a collection of young. There are no 'guardians' of the crèche (SLADEN 1958).

spp.), starvation (not enough food for one or both chicks), and nest desertion (parents failing to return). Generally, chicks in peripheral nests are more prone to predation than those in central nests. At KING GEORGE ISLAND, **breeding success** (in number of chicks fledged per nest) is reported as 0.98 (Williams 1995). After the chicks have fledged (Feb.-Mar.), the adults return to the sea to build up their fat reserves during a pre-moult period (the duration of which ranges from a few days to more than a month), before **moulting** requires them to remain ashore or – more commonly – on ice-floes, and to fast for 15 to 23 days. According to Penney (1967), the period spent on land/ ice-floe includes the pre-moult (5.1 d, in which the penguin's body prepares for shedding its coat), moult (14.9 d, in which the feathers are shed and the new ones pushed out), and post-moult stage (2.5 d, which the birds mainly spend preening and oil-preening their new plumage). During the time spent ashore/ 'a-floe', birds lose approximately 45 % of their initial mass at a rate of 151-193 g per day (Penney 1967). Peak numbers of moulting adults have been recorded in early March (Williams 1995), with unsuccessful breeders moulting earlier and immatures completing their moult before non-breeders and breeding adults. In a study at Cape Crozier, the modal **age of first breeding** was five to six years (Ainley 2002), with the average age for females being 5.0 years and for males 6.2 years. Females, but not males, may breed at three years of age. **Survival** varies annually; and mortality is higher in females than in males (Ainley & deMaster 1980) so that the sex ratio becomes male-biased with age, changing from 1:1 for two-year-olds to 1:0.4 in 14- to 16-year-olds (Ainley & al. 1983). Most adult mortality occurs during the winter (Spurr 1975c). Moreover, not all penguins that survive and return to the colony will also return to breed. Spurr (1975c) reported that during an observation period of three years, between 4 % and 26 % of the males and 2 % and 18 % of the females which had previously bred returned the following year but did not breed.

3.1.4 Ethogram[24] of Adélie Penguin Behaviour During the Reproductive Period

In the following section, an overview of Adélie penguin behaviour during the reproductive period is given.

N.b.: Whenever PERSONAL OBSERVATIONS differed from or contributed to these accounts, they will be presented directly below the respective passages extracted from the literature. Likewise, METHODOLOGICAL CONSIDERATIONS pertaining to categorisations used in THIS THESIS are mentioned to avoid misapprehensions concerning chapter 4.

The **displays**[25] **and breeding behaviour** of Adélie penguins are well known, with main studies by Levick (1914), Sapin-Jaloustre & Bourlière (1952), Sladen (1958), Sapin-Jaloustre (1960), Penney (1968), Ainley (1975), and Spurr (1975b). Supplementary work has been contributed by, e.g., Spurr (1975c), Ainley (1978), Bekoff & al. (1979), and Müller-Schwarze & Müller-Schwarze (1980), while reviews have been presented by Jouventin (1982), and Marchant & Higgins (1990).

Visual signals involving head feathers and eyes are important components of displays, and of all penguin species, the Adélie penguin has the richest repertoire of such optical signals (Jouventin 1982). Historically unsurprising, yet scientifically inconvenient, different authors have

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[24] Ethogram (Broom & Johnson 2000, p. 176): A detailed description in space and time of each behaviour shown by members of a particular species.

[25] According to Spurr (1975b, p. 473), an act may be called a display only, if it conveys a signal to another animal and if it seems to be specially adapted for that function.

attributed different names to the penguins' displays observed in different species. Jouventin (1982) collected contributions of the respective authors as part of his comparative examination of penguin visual and vocal signals, their evolution and adaptive characters. Spurr (1975b, c) investigated communication in adult Adélie penguins as well as the behaviour of Adélie chicks. Ainley (1974, 1978) focused on comfort behaviour of Adélie and other penguins as well as on activity patterns and social behaviour of non-breeding Adélie penguins, and together with M. and A. Bekoff (Bekoff & al. 1979) took a particular interest in the ontogeny and organisation of comfort behaviour in Adélie penguins.

3.1.4.1 Breeding Behaviour

Descriptions of the main displays in pair-formation and -maintenance have been taken from Jouventin (1982), as were the alternative names and their respective authors which are given in brackets. Additionally, some behaviours which do not meet the criteria of displays were examined in this study, and these, too, are listed below.

3.1.4.1.1 Ecstatic Display

> "As was shown for the Adélie penguin, in which the **ecstatic display** is the most outstanding and the cycle[26] the most contracted, a more complex ecstatic display confers an evident adaptive advantage, for the pair-formation period is the only one which can be hastened." (Jouventin 1982, p. 105)

The **ecstatic display** (Wilson 1907, as quoted in Jouventin 1982; = 'position extatique', Sapin-Jaloustre & Bourlière 1952, p. 11) is performed mainly by lone males on the territory, functioning to advertise the nest-site to unpaired females, rarely by females (Derksen 1977; Sladen 1958; Spurr 1977). The bird "stretches out [(fig. 3-3)], raising head and bill vertically and, vibrating its chest, claps its bill repeatedly while synchronously flapping its flippers perpendicular to the body" (Jouventin 1982, p. 19). The ecstatic display is "accompanied by loud, distinctive vocalisation increasing to a climax, with feather crest raised and sclerae exposed" (Williams 1995, p. 175). Jouventin (1982, see quote) points out that among the different penguin species, a greater complexity of the 'ecstatic display' is positively correlated with a shorter pair-formation period and a higher level of synchronicity with respect to the beginning of the breeding cycle.

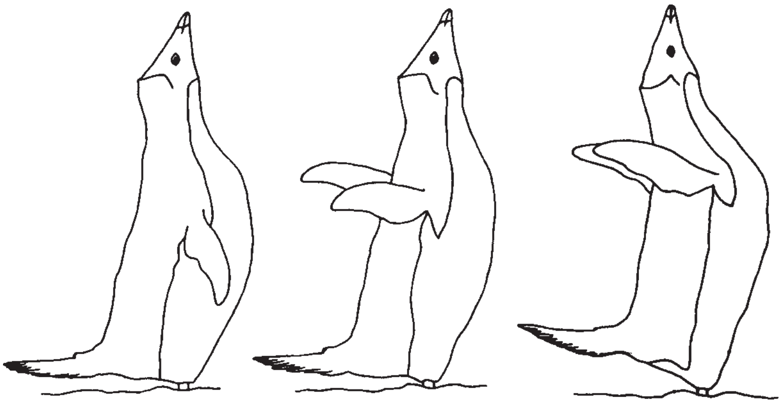

Figure 3-3: Three Different Stages of the Ecstatic Display. Bill clapping (cf. text) not depicted. From Spurr (1975b)

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[26] breeding cycle

PERSONAL OBSERVATION: As THIS STUDY started after the majority of pair-bonds had been formed, the ecstatic display was only occasionally observed. If it occurred, however, it appeared to be ‘contagious’; for after one penguin started, he[27] was usually soon joined by others. This behaviour was frequently recorded under circumstances of general ‘unrest’, e.g., intense fights in the neighbourhood or considerable conspecific movement both in- and outside the colony.

3.1.4.1.2 Bowing

Bowing (ROBERTS 1940; SLADEN 1958) is performed during pair-formation (‘oblique stare bow’, PENNEY 1968), by pairs during nest relieves (= change-overs), by males prior to copulation, and following disturbances or quarrels. “The head is usually lowered approximately half way to the ground, in front of the body. The flippers remain by the side. The display is silent, with the bill closed.” (SPURR 1975b, p. 467; also see fig. 3-4). “Bowing becomes less frequent as the pair grows better acquainted, this gesture evidently playing a role in lessening partner aggressiveness. Bowing occurs much more rarely out of context than do ecstatic or mutual displays” (JOUVENTIN 1982, p. 27).

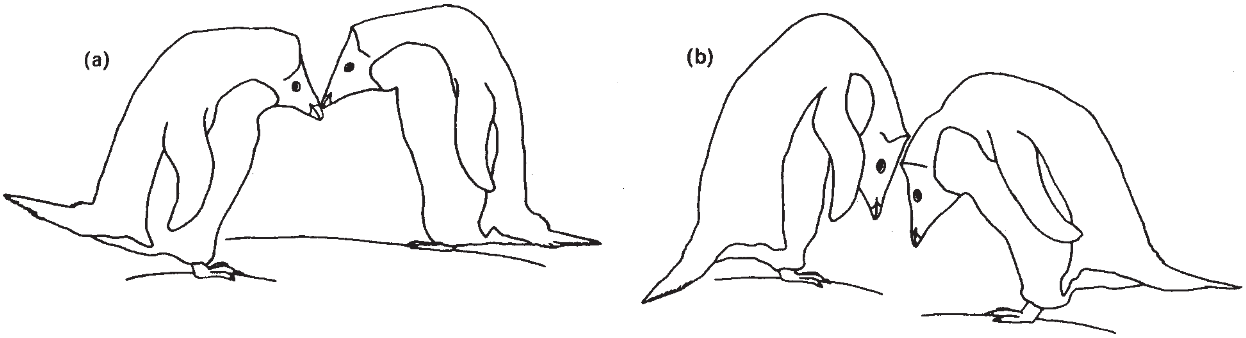

Figure 3-4: The Bow. (a) shallow, (b) deep. From SPURR (1975b)

PERSONAL OBSERVATION: In THIS STUDY, bowing was most frequently observed during nest relieves (change-overs).

3.1.4.1.3 Mutual Display

The **mutual display** (= ’parade mutuelle’, SAPIN-JALOUSTRE & BOURLIÈRE 1952; ‘mutual epigamic display’, ROBERTS 1940) is usually performed by pairs at the nest (WILLIAMS 1995). “Mutual display is not present at the beginning of a pair-formation but generally occurs between well-acquainted partners or between parents and chicks” (JOUVENTIN 1982, p. 27). The birds are facing each other in a posture similar to the ecstatic display, but with their flippers held at the side. The mutual display is performed on two levels of intensity: It is either associated with distinctive loud vocalisation (fig. 3-5; loud mutual display, SLADEN 1958) or with quieter, soft calls and less pronounced movements (fig. 3-6; quiet mutual display, SLADEN 1958). Mutual displays and (mutual) bowing are shown most often alternately during nest relieves of the incubating or brooding bird. The importance of (loud) mutual displays for individual recognition has been shown by SLADEN (1958), and was experimentally confirmed by PENNEY (1968). JOUVENTIN & ROUX (1979, as quoted in JOUVENTIN 1982, p. 27) were able to determine “by preventing birds from singing or by modifying the aspect of the oncomer [sic] that identification was vocal and not optical”.

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[27] Given that this behaviour is predominantly shown by males, the male pronoun is used on this occasion.

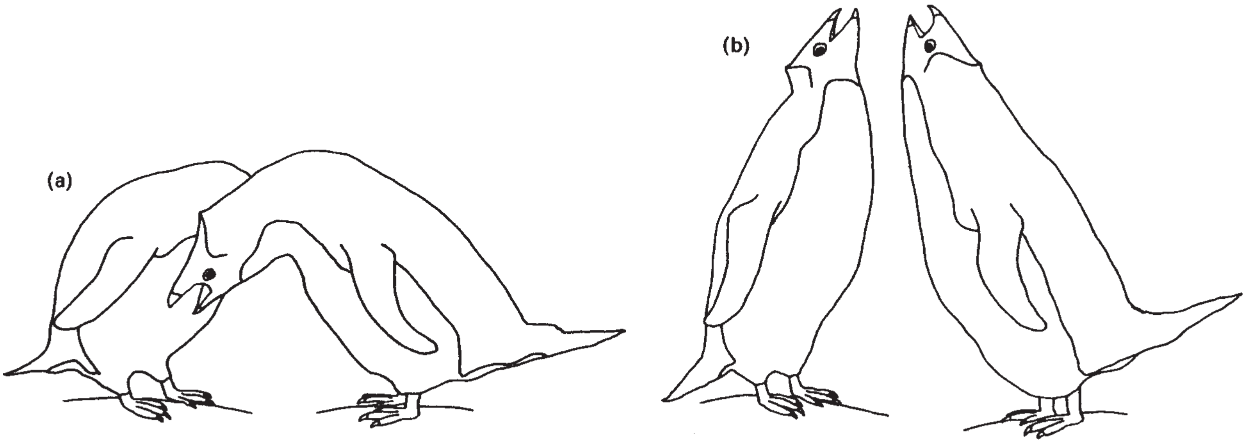

Figure 3-5: Loud Mutual Display by a Pair of Penguins. (a) initial bending, (b) final head waving. From Spurr (1975b)

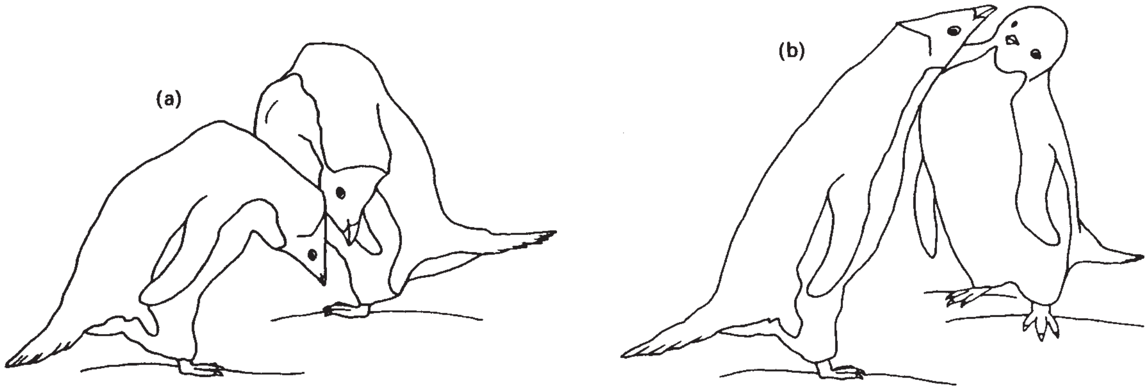

Figure 3-6: Quiet Mutual Display. (a) initial bending, (b) final head waving. From Spurr (1975b)

<u>PERSONAL OBSERVATION</u>: In this study, mutual display was observed most frequently during nest relieves, both just prior to the actual change-over, but also after that, when the relieved partner would return for an indefinite number of times to add new stones to the nest.

<u>METHODOLOGICAL CONSIDERATION</u>: Due to colony-camera distance, no distinction between loud and quiet mutual displays was attempted.

3.1.4.1.5 Nest and Egg/ Chick Manipulation

Nest manipulation involves all actions that serve to actively maintain the nest. This definition excludes behaviours of a defensive agonistic nature (which also help maintain the nest by discouraging others to dismantle it). The actions subsumed under nest manipulation included adding new pebbles (bill), rearranging existing ones (bill), and scratching the nest bowl (feet). While the latter could be combined with a number of head and neck positions[28], the bird's head was down to perform the former two, with the neck pulled in or elongated and the bill touching or close to a nest[29]. The bird was either prone or up, focusing on something inside or close to their nest (i.e. potential new nest stones in the vicinity or the neighbouring nests).

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[28] and has been recognised to contain, at least shortly after arrival at the colony, a proprietary element, rendering it a communicative signal rather than a body movement for nest maintenance: "Between calls the newly arrived, older bird occasionally lies down in the old nest depression and Scratches, a behavior [sic] that indicates ownership of a specific site." (Ainley 1975, quote taken from Ainley & al. 1983, chapter 5, p. 78)

[29] not necessarily their own…

Egg or chick manipulation is similar in appearance, but the behaviour is exclusively focused on the nest interior. Eggs (or small chicks) are turned or otherwise rearranged with the help of bill and/ or feet. During egg and chick manipulation, the bird is mainly up, with their head down, their neck pulled in or elongated and their bill touching or close to the nest's contents. When prone, the bird achieves a limited amount of manipulation by shuffling and shifting on the eggs (or small chicks).

Figure 3-7: Nest Manipulation. © H. Worth

Figure 3-8: Egg Manipulation. © H. Worth

METHODOLOGICAL CONSIDERATION: Being mainly concerned with maintenance of the nest and its contents, these behaviours were examined with respect to their susceptibility to disturbance. They are not mentioned in Jouventin (1982), as they do not (consistently) represent 'signals' to another penguin individual. For the same reason, they are not considered displays.

3.1.4.2 Resting Behaviour

> «Le Manchot en position de repos s'abandonne-t-il à un vrai sommeil avec perte de conscience du monde extérieur? Il nous a semblé que oui, tout au moins dans la position couchée, car on peut s'approcher de lui, le photographier et le filmer sans qu'il réagisse. Par contre, dans la position debout, le Manchot réagit au moindre bruit, en particulier au déclic d'une camera et il nous a été impossible de le filmer de près dans cette attitude.»
> (Sapin-Jaloustre 1960, p. 92) [30]

PERSONAL OBSERVATION: Resting behaviour is generally characterised by a lack of motion, as well as by a lack of observable attention to external stimuli. The birds are either prone (fig. 3-9 a) or up (sitting or standing, fig. 3-9 b), with their eyes closed or open, but not widely open. This distinction can be made, because Adélie penguins expose the white sclerae when opening their eyes widely, and this feature contrasts starkly with the black feathers of the head [31].

Unless the birds are dozing or soundly asleep, resting behaviour may infrequently be punctuated by **small movements**[32]. Among these are **yawning** (a comfort behaviour, see there; fig. 3-10 c, d), **swallowing**[33] or brief **shuffles** ('rocking' on the nest, i.e., nest/ egg manipulation performed while prone, to achieve a more comfortable position on the nest). A further behaviour, termed **bill-tremor** or **bill-shake** (depending on intensity, with smaller movements for the former), was likewise considered a small movement. On one occasion (FA X2-1, 26.11.2001 morning, pre-visitation), a

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[30] "The resting penguin – does he lose himself into true sleep with loss of consciousness towards the outside world? With respect to the prone position, this seemed to us to be more or less the case, for it was possible to approach, to photograph and to film him without eliciting any reaction. In contrast, in the upright position, the penguin reacted to the slightest noise, in particular to the trigger of a camera, and it was impossible for us to film him close up in this attitude/ behaviour." (Transl. by K.Schuster)

[31] … while the white ring of feathers merely allows for detection of the eye from a distance.

[32] cf. Fraser & Broom (1990): comfort-shifts

[33] termed 'head-bob' by Ainley (1974, p. 23) who declares it "not a true comfort behaviour"

behaviour termed ‘**bill-rest**’ was observed during a preening bout (see comfort behaviour) while the bird was prone. This behaviour was characterised by the bird’s bill being tucked in at (above) the elbow and remaining motionless for periods of up to 48 seconds before either succumbing to gravity and dropping to the ground (‘bill-drop’; often startling the bird) or being replaced by a short (one to seven seconds) period of vigilance usually caused by movements in the bird’s immediate vicinity (e.g., a nearby conspecific standing up). Bill-rest was then resumed either directly or after one to three seconds of preening. The posture of ‘bill-tucked-behind-wing’ is comparable to that of ‘head-tucked-under-wing’ employed by flying birds and thus constitutes a resting behaviour[33].

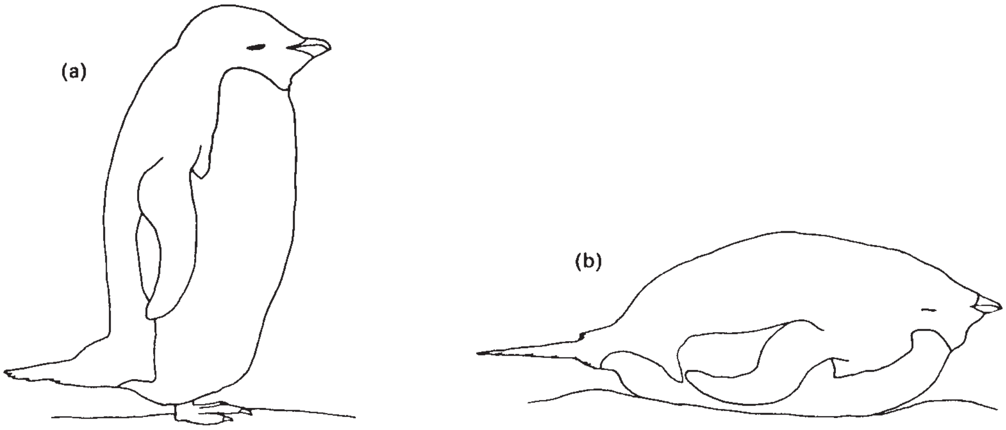

Figure 3-9: Resting. (a) Standing up, (b) lying down (prone). From Spurr (1975b)

METHODOLOGICAL CONSIDERATION: In this thesis, the term ‘resting behaviour’ combines the categories ‘at **rest**’ and ‘**asleep/ dozing**’, as it was impossible to unequivocally distinguish these on the videotape.

3.1.4.3 Comfort Behaviour

> “Comfort behaviour includes movements of shaking, stretching, cleaning, preening and washing.” (McKinney 1965, as quoted in Ainley 1974)

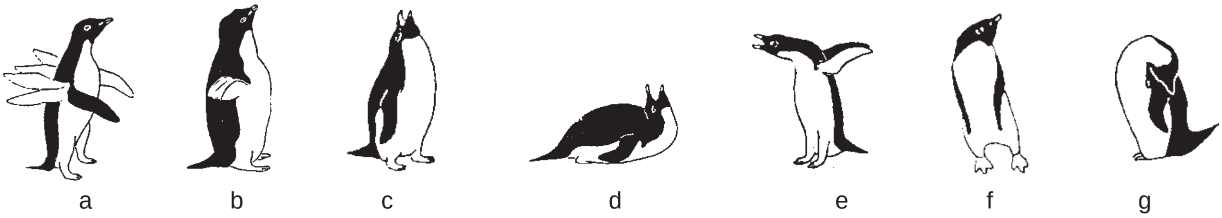

Figure 3-10: Various Comfort Movements. a) Rapid-wing-flap, b) Ruffle-shake, a ruffling of the feathers with extension of the neck and slight back and forth wing movement, followed by a body-shake, c) Yawn, upright, d) Yawn, prone, e) Both-wings-stretch, segment 1, f) Both-wings-stretch, segment 2, g) Shoulder-rub – a Cleaning or a Preening Movement. From Ainley (1974)

In his paper ‘The comfort behaviour of Adélie and other penguins’, Ainley (1974) gives both a comprehensive overview and exact descriptions of the behaviours concerned. Rather than trying to rephrase Ainley (1974), this thesis quotes his descriptions verbatim, unless indicated otherwise (e.g., parentheses, comments pertaining to this study). Only behaviours relevant to incubating penguins, however, are listed in the following section.

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[33] albeit not a very restful one…

3.1.4.3.1 Rapid-Wing-Flap

The **rapid-wing-flap** is a shaking movement predominantly involving the wings: “The wings move as far ventrally then dorsally as anatomically possible and with such force and rapidity that a ‘whirr’ is audible[34] . During the least vigorous bouts the wing movement is 6.6 cycles per second. However, at the normal rate it is too rapid to be counted visually. The body and neck are stretched upward, and the feet shuffle about to help maintain balance” (Ainley 1974, p. 25; also see fig. 3-10 a). “The feathers are sleeked. The behaviour often merges into or out of the both-wings-stretch” (ibid., p. 25, also see below). “Rapid-wing-flap is performed after long periods of inactivity and [– less important with respect to incubating birds –] after vigorous activity (e.g., swimming)” (ibid., p. 25).

3.1.4.3.2 Ruffle-Shake

The **ruffle-shake** is a shaking movement which involves the whole body[35] . “While the neck stretches fully upward, the feathers of the entire body, neck and head are ‘ruffled’ […] beginning with the nasal, ocular, and occipital crests of the head” (Ainley 1974, p. 25; also see fig. 3-10 b). “When the neck begins to pull back down, there occurs a slight headshake [(see below)] and an intermediate wing-flap. Both grade into the rotary movement of a body-shake. The wing movement is performed with 1/3 of the potential excursion of the wings at 4.5 cycles per second, and hence is a reduced version of the rapid-wing-flap. After the body-shake [sic], the feathers are relaxed […]. Tail-wags[[36]], and/ or head-bobs[[37]] sometimes follow. Ruffle-shakes are performed during and following long bouts of preening” (Ainley 1974, p. 25f.).

<u>PERSONAL OBSERVATION</u>: Apart from the situations described in Ainley (1974), ruffle-shakes were found to frequently occur after an incubating bird changed their posture from prone to upright.

3.1.4.3.3 Yawn

The **yawn** is a stretching movement. “The bill opens to the fullest extent for about a second while the head, sunk on the shoulders, tilts back. As the bill closes, the head returns to normal positions. Yawns may occur in prone […] [(fig. 3-10 c)] or upright […] [(fig. 3-10 d)] birds. Frequently several yawns occur in succession. They also occur as part of the both-wings-stretch (see […] [there]), but in that association the neck stretches fully and usually upwards. The bill remains open longer when the movement is part of the both-wings-stretch than when it is performed alone” (Ainley 1974, p. 26).

3.1.4.3.4 Both-Wings-Stretch

Apart from the head-scratch (see below), the **both-wings-stretch** is the most often described avian comfort movement (Ainley 1974). The both-wings-stretch is a stretching movement consisting of “two segments which sometimes occur independently of each other. In the first segment […] [(fig. 3-10 e)] legs and body are stretched so that the body is almost vertical and the feathers are sleeked […]. The tail is stretched downward, the neck is stretched upward and sometimes slightly forward, and the bill is often opened in a yawn. The wings are thrust backward until the tips almost touch behind the back. Segment one is held for a few seconds and then merges into segment two.

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[34] as long as the observer is close enough to the penguin to hear it…

[35] It is not called a body-shake, for “[b]ody-shakes are performed to remove water from the body. After a few body-shakes and headshakes, the birds perform ruffle-shakes.” (Ainley 1974)

[36] side-to-side movements of the tail, not separately evaluated in this thesis

[37] head movement caused by swallowing

In segment two […] [(fig. 3-10 f)] the bill usually closes although it still points upward. The head is withdrawn to the shoulders and the wings are brought against the flanks and lower abdomen. The legs and body remain stretched upward and the tail remains stretched downward. Segment two is held for a few seconds and often ends with a sneeze[38] or headshake. The feathers are then relaxed" (ibid., p. 27f.).

According to Ainley (1974), the both-wings-stretch is sometimes performed by prone birds, but more usually observed after a penguin rises from a long period of inactivity, such as incubation. "Rapid-wing-flap and this behaviour often merge into one another so that a rapid-wing-flap occurs between the two segments of the both-wings-stretch" (ibid. p. 28).

3.1.4.3.5 Headshake[39]

The **headshake** is a shaking movement that does not extend below the neck. During the performance of a headshake, "[t]he head flicks from side-to-side perpendicular to the body axis" (Ainley 1974, p. 19; also see fig. 3-11). "These lateral movements vary in number, speed and amplitude. Headshakes remove [salt gland fluid[40]], water, food, dirt, snow, […] and other foreign matter from the head and bill. They are characteristic of birds which have just emerged wet from the sea; of parents which have just regurgitated food to chicks; of birds hit in the head by feces squirted from a neighbouring bird; and of birds which have sneezed […]" (ibid., p. 19). "One of the most common usages of the headshake by a penguin is to flick drops of salt gland fluid from the bill tip where they normally form" (ibid., p. 20).

Figure 3-11: Headshake – a Side-to-Side Movement. From Ainley (1974)

<u>PERSONAL OBSERVATION</u>: In addition to the headshake described in Ainley (1974), recordings for this thesis identified a **head-shoulder-shake**, during which the shaking movement extended beyond the neck, but did not include the whole body (see ruffle-shake). As the gradation between headshake and head-shoulder-shake was frequently fluent, however, these two were regarded as sub-categories and were not evaluated separately.

3.1.4.3.6 Cleaning and Preening

While **cleaning** movements serve to remove 'foreign matter' and allow various parts of the body to be employed as 'cleansing agents' (e.g., the foot in 'head-scratch', see below), **preening** serves to keep in order and maintain the plumage using head and/ or bill; it is defined as involving "contact of the bird's bill and head with the feathers" (McKinney 1965 as quoted in Ainley 1974) – except in the wing- and shoulder-rubs (which despite of lacking bill-contact are also considered preening movements in the context of oil-preening; see below). According to Ainley (1974), McKinney (1965 as quoted in Ainley 1974) differentiated three types of preening for Anatidae, a classification that Ainley adopted for penguins: oiling, nibbling and washing. "Oil-preening [(see below)] includes transfer of oil to the feathers from the uropygial gland at the base of the tail. Nibble-preening [(see below)] includes any treatment of the feathers without use of oil or water, while washing includes

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[38] As this behaviour is identified by sound, it is not included in this study.

[39] spelt head-shake in Ainley (1974)

[40] order rearranged, as salt gland fluid (original position indicated by […]) was deemed to be not a foreign matter

feather nibbling in the water during bathing[[41]]" (ibid., p. 30). Ainley (1974) stated that oil-preening was almost always performed after the birds emerged from the sea (i.e., on wet plumage). In their study on the ontogeny and organisation of comfort behaviour in Adélie penguins, Bekoff & al. (1979) examined both oil-preening[42] and nibble-preening[43] in dry[44] birds.

The main difference between oil- and nibble-preening is that the former serves to spread oil over the bird's plumage, while the latter behaviour does not involve any distribution of oil but serves to keep the 'lay-out' of the plumage in order (thereby improving insulation). The motor pattern and sequences, however, are the same (Ainley 1974). "When **oil-preening** begins, oil is distributed to the feathers by several movements, including a strict three movement sequence that transfers oil from the uropygial gland to the head and bill" (ibid., p. 31f.). Using the oil-covered head and bill, the bird then continues to spread oil across their plumage, preening with the bill wherever the plumage can be accessed that way, and rubbing their head on shoulders and wings to cover the remaining surface.

With the exception of the wings, which are usually taken care of once the bird is back in the colony; oil preening is mainly observed after Adélie penguins have left the water and before they enter the colony. At the nest site, however, "Adélies commonly preen by nibbling; sometimes for 5-10 minutes during which the bird preens one or several spots, or even for most of an hour during which many parts of the body are preened. **Nibble-preening** is performed during periods of little other activity. In fact, Adélies often doze for short periods during a bout and often the bout ends when the bird falls asleep" (ibid., p. 38).

Depending on context, the **shoulder-rub** is a cleaning or a preening movement. "The bird rubs the back or side of the head against the shoulder (Ainley 1974, p. 28; also see fig. 3-10 g). "It is often performed after a bird emerges from the sea to remove water from the shoulder, upper back and head" (ibid., p. 28). "In other [(dryer)] contexts it removes foreign material from the head or shoulder" (ibid., p. 28). "It is also performed during oil-preening to distribute oil to the shoulder" (ibid., p. 28).

Similar to the shoulder-rub, the **wing-rub** may also be a cleaning or a preening movement. "The wing is raised from the side to project straight out or slightly upwards and backwards. The back, side, or top of the head, or throat is then rubbed on the wing's leading edge which is held uppermost (ibid., p. 29; also see fig. 3-12). "During oil-preening it functions to distribute oil on the feathers of the head after oil has been transferred from the uropygial gland to the wing edge" (ibid., p. 29).

Figure 3-12: Wing-Rub – a Cleaning or a Preening Movement. From Ainley (1974)

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[41] and consequently does not apply to the penguins studies for THIS THESIS

[42] which they termed "dry-oiling" to emphasise that bill contact with the uropygial gland was made and oil was distributed over the dry plumage

[43] which they termed "non-oiling" indicating that no bill contact was made with the uropygial gland

[44] i.e., birds which had been out of the water for at least two hours before observations started

N.b.: To date, no **allopreening** has been reported for Adélie (or indeed any other *Pygoscelid*) penguins[45]. Jouventin (1982, p. 27), however, states that the 'mutual display' (see above) "has the same function[46] as mutual preening in other species."

METHODOLOGICAL CONSIDERATION: This thesis did not wish to re-examine the fine detail, nor analyse the individual components of preening, but regarded preening as a behaviour during which the bird focused their attention upon their own body rather than on their environment. With the exception of head-scratch (unequivocally a cleaning movement), the behaviours were subsumed in the category 'preening', as preening was considered the 'basic action' while shoulder- and wing-rubs (cleaning or preening movements) were frequently observed in conjunction with it.

3.1.4.3.7 Head-Scratch

The **head-scratch** is a cleaning movement. "Before scratching, the bird changes its centre of gravity so that it is supporting itself on one foot and its tail. It then arches its body toward the free foot and extends the neck downward. Finally it brings the free foot over the depressed flipper and scratches the head with a quick up-down motion" (Ainley 1974, p. 29; also see fig. 3-13). "The free foot is always brought to the same level and thus the part of the head to be scratched depends on the position to which the head is lowered" (ibid., p. 29). Head-scratching is performed "independently of other behaviours but often occurs during bouts of intensive preening" (ibid., p. 29).

Figure 3-13: Head-Scratch. From Ainley (1974)

3.1.4.4 Vigilance Behaviour

> "If they had become aroused by my presence 10 m away, they would have raised their heads, opened their eyes widely, and looked quickly about." (Ainley 1974, p. 2)
>
> "A sudden or strange sound of any kind does indeed cause all birds of a colony to become alert." (Ainley 1974, p. 23)

Vigilance behaviour conveys the penguin's alertness[47] towards their surroundings. It serves to acquire information on (changes in) the environment and as such is characterised by orienting (looking for and identifying the source) and/ or monocular fixating movements ('keeping an eye on things').

Birds in general have limited mobility of the eyes, and tend to make head movements in contexts where primates would make eye movements (e.g., Walls 1942; quoted in Land 1999). Therefore, scanning (defined in this thesis as comprising repeated head movements of a degree below 45°

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[45] In the genera *Spheniscus*, *Eudyptes*, *Megadyptes* and *Eudyptula*, in contrast, it certainly helps reduce ectoparasites, and may constitute an important element in aggression-reduction, pair-formation and pair-maintenance.

[46] i.e., serves a double function, as other penguins likewise perform 'mutual displays'.

[47] alert: keenly watchful, on the look-out, ready for sudden action (Webster's Comprehensive Dictionary 2003)

performed in quick succession) and head turns (small: 45° to 90°; large: > 90°) can be considered an adequate measure for vigilance in penguins, provided that

a) they are not part of another behaviour system (e.g., head movements during nest-stone rearrangement) and

b) the birds' vision is actually able to capture what is happening around them (s.b., penguin vision).

Intensity of alertness may to some extent be gauged by the velocity, duration and frequency of these movements, while width of angle additionally depends on the penguin's relative position with respect to location of stimulus.

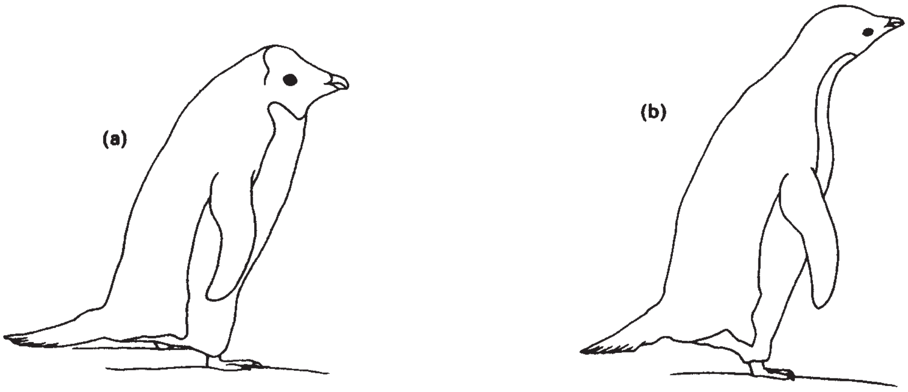

Figure 3-14: Looking Around – Vigilance Behaviour. From Spurr (1975b)

METHODOLOGICAL CONSIDERATION: In this thesis, the following criteria had to be met to consider a penguin alert (rather than engaged in any other behaviour): The bird was either prone or up, focusing on something/ someone outside their nest. The bird's head was level with their body or raised, turning or turned towards the source of disturbance. The eyes were open, the bill closed, and the flippers down. The behaviour element 'head turn' (and scanning phases, s.b.) served to assess intensity of vigilance. According to horizontal expansion, head turns were divided into **large head turns** (> 90°), and **small head turns** (45° > 90°), complemented by **scans** (< 45°). Each of these was further specified by noting the vertical component (forward vs. upward), as well as velocity and duration of the movement. Due to their slight expansion, scans were only considered if the penguin exhibited several of them in short succession (**scanning phase**), or if they appeared in conjunction with other elements. An exhaustive definition of these scanning phases is given in appendix 4-1.

3.1.4.5 Agonistic Behaviour[48]

> "[T]he Adélie penguin exhibits the highest level of aggressiveness of all penguins and has the most varied agonistic repertoire." (Jouventin 1982, p. 94)

In his publication 'Visual and Vocal Signals in Penguins, their Evolution and Adaptive Characters', Jouventin (1982, p. 13) stated that "[i]n the **penguin family**, attitudes[49] can be classified by their degree of increasing aggressiveness". He distinguished the following five 'levels' (ibid., p. 13):

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[48] Descriptions and orthography according to Jouventin (1982), who explicitly states that he retains Spurr's (1975b) classification.

[49] read: behaviours

“**1. displacement activities** showing conflict, such as headshaking followed by swallowing;

2. warning postures such as wing-flapping (which can be integrated into more complex attitudes such as the ‘alternate stare’, [see below]);

3. attitudes based on a lateral movement of the head revealing a low level of aggressiveness and acting as an alarm signal regarding intruders, such as the ‘horizontal head-circling motion’ in the Emperor and the ‘bill-to-axilla’ in the Adélie penguin ([see below]);

4. attitudes based on the rotation of head around bill, showing a mean level of aggressiveness, and constituting a threat signal just before an attack, such as the ‘alternate stare’ of the Adélie penguin ([see below]) and the ‘twisting’ of the genus *Spheniscus*; and

5. variable combat techniques depending on position and size of the birds”.

In the **Adélie penguin**, aggressive interactions are common before egg-laying and during the reoccupation[50] period, especially between birds without established territories (Williams 1995). Threats and charges are often directed against skuas, by both adults and chicks (Williams 1995). The agonistic behaviour observed in Adélie penguins represents a continuum of aggressive displays which occur with increasing intensity from defensive threats to direct attack (fig. 3-16), related to closeness and speed of movement of opponent (Williams 1995). “Depending on the enemy’s distance, a sequence of agonistic actions unfolds and may end in a real attack” (Jouventin 1982, p. 11; but see below for nest-bound birds). Note that for ‘descriptive exactitude’ the following passage adheres to Jouventin’s (1982, p. 11f.) phrasing wherever possible; boldface has been added in this thesis.

During performance of the **bill-to-axilla** attitude (BTA; fig. 3-15 a), “the penguin puts its bill under one wing and grunts while whirling its head. This is often used to signal to distant congeners[[51]]. It is all the more ritualized in that it does not recall a fighting movement and is not necessarily directed towards an adversary” (Jouventin 1982, p. 11). The bill-to-axilla attitude “is not only observed after threats against intruders but also after a typically sexual attitude, the ‘ecstatic display’. The association of these two apparently functionally different attitudes” (ibid., p. 12) can also be observed in other species of penguin. Jouventin (1982, p. 12) concludes that this confirms “the strong relationship between sexuality and aggression”.

Performance of the **sideways stare** (SST; fig. 3-15 b) may occur in prone or upright position. Birds turn their head sideways and stare with one eye at the intruder. “If the intruder moves closer still, the **alternate stare** [(AST fig. 3-15 c)] follows: the bird slowly turns its head from side to side staring with first one eye, then the other” (ibid., p. 11).

“If the intruder comes very close to the bird, the bill is stretched still further forwards, the crest is erected and the pupil of the eye is lowered to reveal the white [of the sclerae]” (ibid., p. 11). This attitude is termed the **point** (P; fig. 3-15 d). “The penguin prepares to attack by opening its bill” (ibid., p. 11). This is termed the **gape** (G; fig. 3-15 e). The bird “then charges the adversary with wings half-opened” (ibid., p. 11), a movement, which (perhaps not surprisingly) is called the **charge** (C; fig. 3-15 f).

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[50] The term *reoccupation period* is used, because adults who lose their eggs will leave their nests for a period of time, but return to *reoccupy* their nest sites approximately when eggs successfully incubated by other penguins begin to hatch (Ainley 2002, Sladen 1958).

[51] conspecifics and other members of the genus *Pygoscelis*

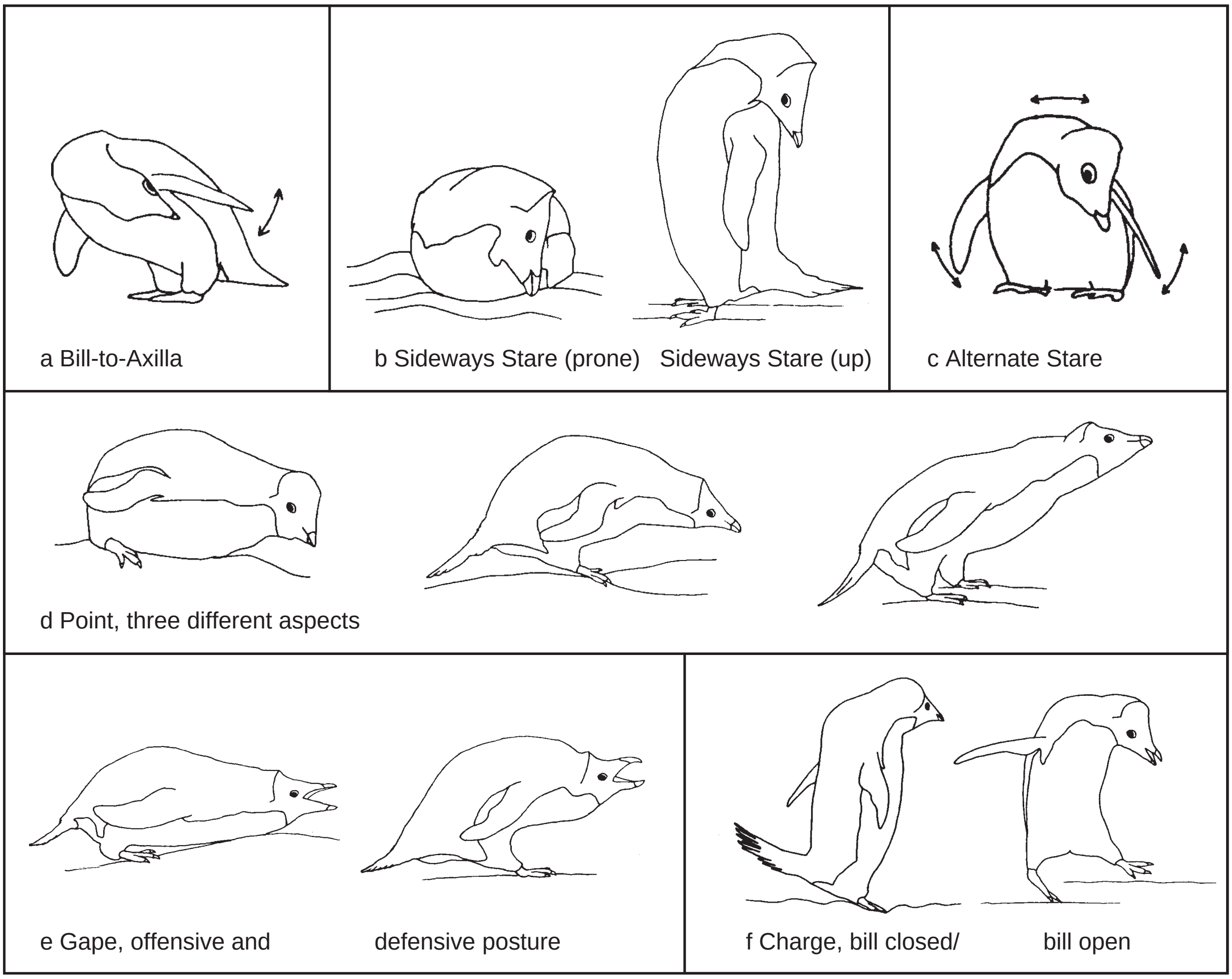

Figure 3-15: Threat Displays. a) Bill-to-Axilla*, b) Sideways Stare#, c) Alternate Stare*, d) Point#, e) Gape#, and f) Charge#. In all attitudes, occipital crest is raised. From *Ainley (1975), #Spurr (1975b)

If the opponent does not withdraw, the penguin “pinches the adversary” (ibid., p. 11), a movement called the **peck** which is also often aimed at birds passing or lingering near the nest, “pushes [the other penguin] in the chest” and strikes at them with the wings (termed **full fighting**). In incubating birds, the element of ‘charge’ will rarely be observed, as it would involve leaving the nest and thus exposing the eggs and/ or chicks to the cold as well as to predatorial eyes. Instead, **bill-jousting** or **tête-à-tête** behaviour occurs, especially between birds on adjacent nests: “Two neighbours take a firm stand on their nests and face each other, head forward and bill open. Each sporadically tries to grab the adversary’s bill” (ibid., p. 11) with their own and twist it.

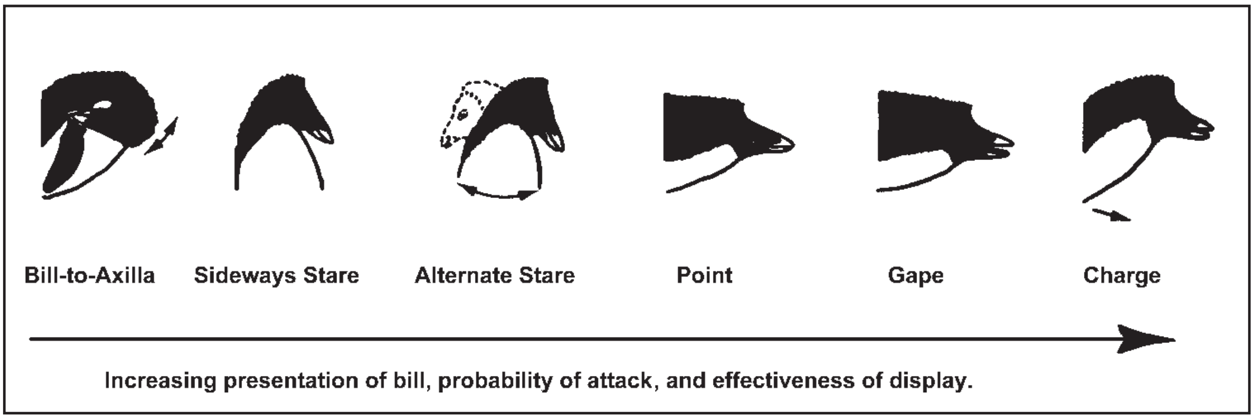

Figure 3-16: Gradation of Threat Display. From Spurr (1975b)

PERSONAL OBSERVATION: In addition to being employed to settle neighbour conflicts, 'bill-jousting/ tête-à-tête' behaviour was also occasionally observed between an incubating bird and a conspecific that approached 'too close for comfort'.

METHODOLOGICAL CONSIDERATION: With the exception of 'charge' and 'full fighting' (the two behaviours difficult to perform while sitting tight on eggs), the behaviours described above were adopted as sub-categories for the parameter agonistics in THIS THESIS. The contact-behaviour 'peck', however, was grouped with the non-contact-behaviours 'point' (if bill was closed) and 'gape' (if bill was open), for distance and angle of observation frequently prevented the (lack of) space between bill and body to be unequivocally recognised.

3.1.5 Physiology

N.b.: While the previous chapter (section 2.3) provided information on disturbance-related information on behaviour and heart rate, this section focuses on the physiological basis of penguin vision and heart rate.

The capacity to adequately perceive disturbance stimuli is a prerequisite for responding to them; and evolved physiology determines the range of possible responses (e.g., heart rate increases/ decreases during predator presence).

Firstly, studies investigating penguin vision in air and water are briefly reviewed. Next, the electrocardiogram (ECG) of vertebrate heartbeats is very quickly recapitulated. Following, an overview of penguin heart rate values during resting and maximum activity is presented. The overview draws on studies by various authors not primarily interested in the emotional component of heart rate. These values are thus suggested to constitute a 'robust frame of physiological capability', i.e., the penguins' emotional heart rate responses would be expected to fluctuate within these boundaries.

3.1.5.1 Penguin Vision

> "Recent research indicates there's more to penguins than meets the eye. If you've ever wondered what it would be like to be able to see as clearly under water as you can on land, just ask the nearest penguin." (SIVAK[52])

Contrary to common belief, penguins are emmetropic (in focus) in air, with a trend towards slight myopia (short-sightedness), while moderate hyperopia (far-sightedness) exists in water (SIVAK & MILLODOT 1977; SIVAK 1980). The penguin cornea has a flattened shape which results in a relatively small alteration of refractive state upon changing between air and water medium[53]. Moreover, an early study of the anatomy of Adélie penguin eyes (SIVAK & VRABLIK 1979) indicated that an accommodative mechanism can compensate for refractive losses in water and thus cause emmetropia in both mediums. Accommodative compensation is thought to occur by changes in the shape of the lens brought about by contraction of the ciliary and iris sphincter muscles (HOWLAND & SIVAK 1984).

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[52] http://ccirserv2.uwaterloo.ca/sivaklabs/AboutUs_Penguins.html (accessed: 04.04.2008)

[53] In comparison, for human eyes there is an approximate change of 40 dioptres (=dioptries) due to loss of refractionary power of the lens (SIVAK & MILLODOT 1977).

For several penguin species, existence of a binocular field has been demonstrated in air[54] (e.g., King penguin, *Aptenodytes patagonicus*: Martin 1999; Humboldt penguin, *Spheniscus humboldti*: Martin & Young 1984, quoted in Martin 1999). As the penguin's eyes are laterally placed, however, the monocular (= lateral) fields of vision are heavily relied upon for various tasks including scrutinising of stimuli and novel objects.

METHODOLOGICAL CONSIDERATION: For the penguins studied, the prerequisite of adequate stimulus perception was thus assumed to be satisfied.

3.1.5.2 Penguin Heart Rate

> "Measurement of heart rate can be a useful measure of the emotional response of an individual to short-term problems, provided that distinction is made between the metabolic and emotional effects, and that the measurement itself does not cause too much disturbance." (Broom & Johnson 2000, p. 92)

All vertebrates exhibit a similar **electrocardiogram** (ECG) with distinctly negative[55] (P, R, T) and positive (Q, S) spikes[56] (fig. 3-17), labelled with capital letters according to international nomenclature (Penzlin 1980). An ECG represents the summation of the electrical activity in various parts of the heart (Randall & al. 2002). The major components of the ECG reflect atrial depolarisation (P), ventricular depolarisation (QRS), and ventricular repolarisation (T). Each PQRST-event in its entirety represents 'one **heartbeat**'. **Heart rate** is usually reported in **'beats per minute'** (bpm), a value derived from counting PQRST-events over a defined period of seconds (counting interval) and extrapolating the resulting figure to minute-values[57].

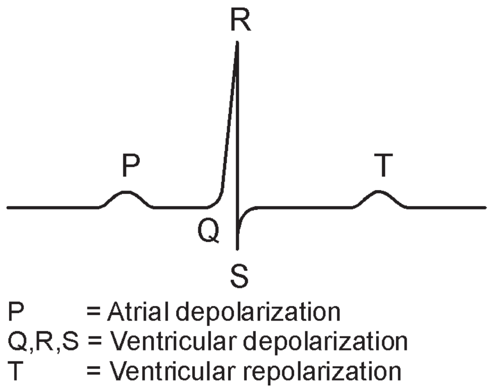

Figure 3-17: Schematic Vertebrate ECG. All vertebrates exhibit a similar electrocardiogram (ECG) with distinctly negative (P, R, T) and positive (Q, S) spikes. From Randall & al. (2002)

As for penguin studies, **counting intervals** mentioned by different authors were found to vary quite widely: Nimon (1997), for instance, used counting intervals of 5 s, 10 s, and 15 s, respectively, in her study on heart rate in Gentoo penguins, *Pygoscelis papua*. For Royal penguins, *Eudyptes*

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[54] Upon immersion, the monocular fields shrink due to loss of corneal refractionary power (caused by presence of the same medium on both sides of the cornea); they cease to overlap, and this results in loss of binocularity in water.

[55] Upward deflection of the spike indicates negativity of the heart's base relative to its tip. [Ausschlag nach oben bedeutet Negativwerden der Herzbasis gegenüber der Herzspitze. (Penzlin 1980, p. 249)]

[56] The ECG of fish and reptiles is characterised by an additional initial spike (V), representing depolarisation of the Sinus (Penzlin 1980).

[57] It is also possible to count a predefined number of heartbeats and subsequently extrapolate the seconds to 1 min.

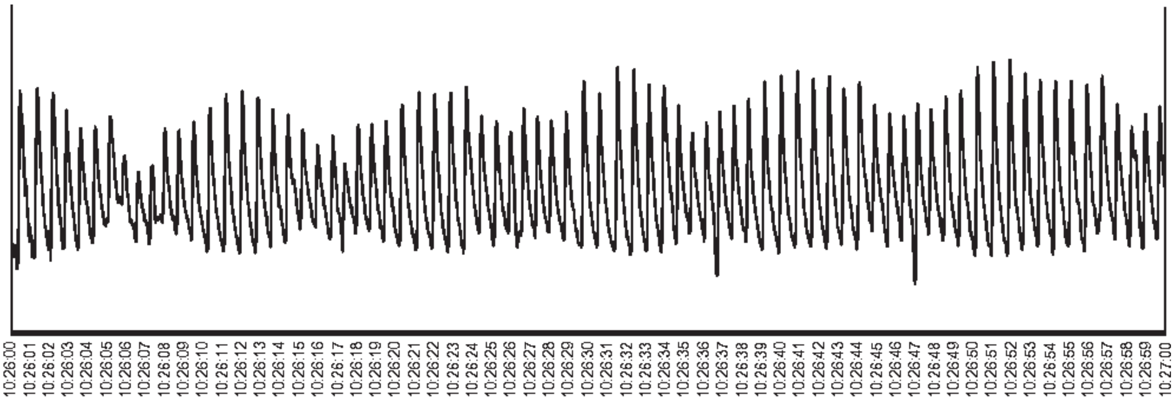
schlegeli, Holmes & al. (2005) extrapolated from intervals of 5 s and 15 s, while Ellenberg & al. (2006, 2009) established intervals of 12 s for Humboldt, *Spheniscus humboldti* and Yellow-eyed penguins, *Megadyptes antipodes*, respectively. DeVilliers & al. (unpubl. data) as well as this study chose 20 s counting intervals for reasons outlined below.

A Brief Excursus on ECG Counting Intervals and Extrapolation Bias/ Error

Different counting intervals capture different aspects of the heart rate actually obtained: Brief to very brief changes in beat-to-beat variability are accentuated in shorter intervals, while longer intervals reflect a longer-lasting response in this parameter. Extrapolation to beats per minute values (bpm), however, creates a 'common currency' which may inadequately represent these different aspects. The following **example** illustrates the results of different counting intervals:

Figure 3-18 shows one minute of resting heart rate containing a total of 77 heartbeats (top), the number of heartbeats counted in successive counting intervals of five different durations, and the derived bpm-values for these counting intervals (bottom).

Differences between consecutive intervals of identical duration primarily arise from the fact that even during rest (no activity, no 'emotional upheaval'), heartbeats do not strictly adhere to a second-by-second pattern and thus do not neatly fit into counting intervals. Rules for incorporation of **'in-between intervals' heartbeats** are therefore set up, and these are used to unequivocally assign the respective beat. Mostly, this will lead to only minor differences from one interval to the next (fig. 3-18: ± 1 beat, as seen between most counting intervals regardless of duration). These



5 s	**6** (72)	**7** (84)	**6** (72)	**7** (84)	**6** (72)	**7** (84)	**6** (72)	**6** (72)	**7** (84)	**6** (72)	**6** (72)	**7** (84)
10 s	**13** (78)	**13** (78)	**13** (78)	**12** (72)	**13** (78)	**13** (78)						
12 s	**16** (80)	**15** (75)	**15** (75)	**16** (80)	**15** (75)							
15 s	**19** (76)	**20** (80)	**19** (76)	**19** (76)								
20 s	**26** (78)	**25** (75)	**26** (78)									
60 s	**77** (77)											

Figure 3.18: One Minute of Adélie Penguin Resting Heart Rate (top), and Heartbeats Counted in Successive Counting Intervals of Different Durations (bottom). Counting the entire 60 s, the sum of heartbeats totals 77 beats. In the bottom part, successive counts and the resulting bpm-values are shown for interval durations of 5 s, 10 s, 12 s, 15 s, and 20 s, respectively.

differences, however, are artificially augmented by extrapolation, and for short intervals may suggest great fluctuations in heart rate when in reality only a gentle undulation occurs.

The size of the **extrapolation bias** increases with increasing shortness of counting interval chosen and equals the extrapolation factor (the factor the counted value is multiplied by; see tab. 3-2). The same applies to ‘truly misassigned’ beats, in that the **extrapolation error** increases with decreasing duration of counting interval/ increasing extrapolation factor.

Table 3-2: Size of Extrapolation Bias for Different Counting Intervals.

Counting Interval	**n Heartbeats Counted → bpm**	**n + 1 Heartbeats Counted → bpm**	**Extrapolation Factor (effecting bpm) ≙ Extrapolation Bias (per beat assigned)**
05 s	06 → 72	07 → 84	12
10 s	13 → 78	14 → 84	06
12 s	15 → 75	16 → 80	05
15 s	19 → 76	20 → 80	04
20 s	25 → 75	26 → 78	03

METHODOLOGICAL CONSIDERATION: In this thesis, heartbeats were counted for 20 s-intervals[58] of heart rate obtained by continuous recording (see section 4.3.3.1.3 for details). To exclude extrapolation bias as well as to minimise extrapolation errors, however, values are presented ‘as counted’, i.e., as beats per 20 s. Comparison to other studies may be effected by tripling values reported here.

Table 3-3 provides **maximum heart rates** measured during various activities, while table 3-4 lists the **resting heart rates** obtained for a number of penguin species. As already mentioned (Theoretical Background, section 2. 3.1.3), the **devices** used to measure heart rate in penguins range from implants requiring surgery before and after the study (e.g., Culik & al. 1990a, 1990b), via subcutaneous electrodes attached to an external recorder (e.g., Culik & al. 1990b, Giese 1998) to equipment the penguin has to make unrestrained contact with (e.g., Nimon 1997; Giese & al. 1999).

Maximum heart rates were measured during or immediately after **terrestrial exercise** and upon resurfacing **after or in-between dives** (tab. 3-3), while **during diving**, heart rate as low as or even considerably lower than resting heart rate was recorded (minimum HR reported: Meir & al. 2008: 3 bpm for an Emperor penguin, *Aptenodytes forsteri*, during a long dive).

Heart rate of (Adélie) penguin chicks is reported to be distinctly higher than that measured for adult penguins regardless of activity (Culik & al. 1990a, 1990b). During **capture** of an adult Adélie, however, Wilson, R.P. & al. (1991) obtained heart rate elevations (from 76 bpm to 287 bpm) the absolute values of which came close to those measured in a chick subjected to the same procedure (from 225 bpm to 310 bpm). Moreover, the difference between resting heart rate and that measured during capture was greater for the adult (increase by 211 bpm) than for the chick (increase by 85 bpm).

In a study on Macaroni penguins, *Eudyptes chrysolophus*, Green & al. (2001) found that **moulting** females exhibited higher resting heart rates than breeding birds of either sex.

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[58] Given that in this study resting heart rates obtained from focal animals were similar to those in humans, this interval length was opted for after consulting an ECG-trained nurse (B. Peleska d.Ä., pers. comm.).

Table 3-3: Maximum Heart Rates of Several Penguin Species during Various Forms of Exercise. Device: Heart rate measuring apparatus; bpm = beats per minute; Specification = type of activity; N = number of animals examined; f.: female, m.: male; poss.: possibly

Species	Species (lat.)	Device	HR active (bpm)	Specification	N	Authors	Year
Adélie	*Pygoscelis adeliae*	implants	287	capture	1	Wilson, R.P. & al.	1991
			287	helicopter approach up to 25m	2		
		external ECG recorder, externally attached electrodes	127 ± 6	stand & preen/ manipulate nest/ rearrange eggs	11	Culik & al.	1989
			127 ± 10	human disturbance	9		
		external ECG recorder, externally attached electrodes	145 (range: 139 - 150)	helicopter overflight at 20m	1	Culik & al.	1990a
Adélie chick	*Pygoscelis adeliae*	implanted telemetric heart rate transmitter	310	capture and weighing	1	Culik & al.	1990b
		a) safety pin electrodes and external ECG (N = 10) and b) implants (N = 4)	276 ± 6	treadmill experiment	1	Culik & al.	1990b
Adélie	*Pygoscelis adeliae*	implants	up to 250	pre-dive	2	Culik	1992
			218 ± 6	post-dive	2		
		implanted arterial catheter and external pressure transducer in watertight chamber	278	mean after vigorous running	3	Millard & al.	1973
Gentoo	*Pygoscelis papua*	implanted arterial catheter and external pressure transducer in watertight chamber	386 (+ 267% resting value)	surfacing post-dive	1	Millard & al.	1973
Humboldt	*Spheniscus humboldti*	implant	245 ± 24	run	3	Butler & Woakes	1984
			231 ± 10	immediately post-dive	3		
Macaroni	*Eudyptes chrysolophus*	moulting females: implants	193 ± 11	treadmill moulting f.	6	Green & al.	2001
		breeding females: external devices	166 ± 7	treadmill breeding f.	9		
		breeding males: external devices	163 ± 5	treadmill breeding m.	9		
Emperor	*Aptenodytes forsteri*	standard ECG submersible recorder (external)	158 - 188	interdive HR; poss. higher (counting programme limitations)	6	Kooyman & al.	1992
		subcutaneous electrodes and external ECG recorder	mean of means: 177 ± 3 (range of means: 97 - 256)	post-dive	9	Meir & al.	2008

Table 3-4: Heart Rates of Several Penguin Species during Rest. Device: Heart rate measuring apparatus; bpm = beats per minute; N = number of animals examined; Specification: circumstances under which resting behaviour was observed, f.: female, m.: male; poss.: possibly.

Species	Species (lat.)	Device	HR rest (bpm)	Specification	N	Authors	Year
Adélie	*Pygoscelis adeliae*	implants	76	not on nest	1	Wilson, R.P. & al.	1991
			83,4	incubating	2		
		external ECG recorder, externally attached electrodes	86 ± 5 (range: 83-91)	prone; at zero windspeed	16	Culik & al.	1989
Adélie chick	*Pygoscelis adeliae*	external ECG recorder, externally attached electrodes	220	sleeping	1	Culik & al.	1990b
			225	resting	1		
		a) safety pin electrodes and external ECG (N = 10) and b) implants (N = 4)	182 ± 11 to 249 ± 5	inside respiration chamber	14	Culik & al.	1990b
			187 ± 5 to 245 ± 5	outside (in cage or colony)	14		
Adélie	*Pygoscelis adeliae*	implants	66.8 ± 1.4	incubating	1	Culik	1992
			77.5 ± 1.6	incubating	1		
		implanted arterial catheter and external pressure transducer in watertight chamber	mean: 122 (min.: 90)	rest stand	3 (1)	Millard & al.	1973
		artificial egg	82.4 ± 8.1 (range of means: 69.5 - 91.7)	rest prone	10	Giese & al.	1999
		external ECG units	82.4 ± 11.7	rest prone	17		
Gentoo	*Pygoscelis papua*	implanted arterial catheter and external pressure transducer in watertight chamber	105	rest stand	1	Millard & al.	1973
		artificial egg	79.5 to 105.8	rest prone	8	Nimon	1997
Humboldt	*Spheniscus humboldti*	implant	121 ± 5	stand on land	3	Butler & Woakes	1984
			139 ± 5	float on water	3		
Macaroni	*Eudyptes chrysolophus*	moulting females: implants	125 ± 12	moulting females	6	Green & al.	2001
		breeding females: external devices	97 ± 2	breeding females	9		
		breeding males: external devices	85 ± 4	breeding males	9		
Emperor	*Aptenodyte forsteri*	standard ECG submersible recorder (external)	mean of means: 72 (range of means: 56 - 80)	stand on land	6	Kooyman & al.	1992
		subcutaneous electrodes and external ECG recorder	mean of means: 73 ± 2 (range of means: 63 - 84)	stand on land	9	Meir & al.	2008

As mentioned in the previous chapter (Theoretical Background, section 2.3.1.3), Culik & al. (1989), found Adélie penguin heart rate to increase linearly with **wind speed** (following the equation HR = 85.8 + 1.35w; with HR = heart rate in beats per minute; w = wind speed in meters per second), but to be unrelated to **temperature**, **humidity**, **cloud cover** and **solar radiation**. The same study reported that (after correcting for meteorological influences) heart rate did not show any **diurnal periodicity**.

Even after such corrections, however, **individual variations in mean resting heart rate** have been found by several authors (e.g., Culik & al. 1989; Giese & al. 1999). Furthermore, in those studies that reported the ‘range of means’ obtained instead of exclusively presenting a ‘mean of means’ (e.g., Giese & al. 1999, Kooyman & al. 1992), variability in mean resting heart rate is seen to be quite extensive: The former authors mention 70-92 bpm for Adélie penguins resting prone, while the latter found mean values between 56-80 bpm for Emperor penguins standing on land.

METHODOLOGICAL CONSIDERATION: In this thesis, heart rate was obtained from the same focal birds over a number of days. As even within-individual resting heart rate showed substantial differences on different days, no attempt was undertaken to ‘average’ heart rate prior to analyses. The effect of wind speed was incorporated by using each animal as their own control (Baldock & Sibly 1990). Ranges will be provided to enable the reader to draw their own conclusions.

3.2 Location: King George Island, South Shetland Islands

> "Antarctica's panhandle, the peninsula survives from a land bridge that once connected with South America. Continents wandering westward and an eastward thrust by the Pacific floor wrenched the original link into a scar of isles and undersea arcs known as Scotia Ridge." (Matthews & Curtsinger 1971)

The **South Shetland Islands** are the group of islands closest to the Antarctic Peninsula. Together with a number of other island groups and the Antarctic Peninsula, they represent the leftovers of a former land bridge between South America and Antarctica (fig. 3-19). Discovered and claimed for King George III as 'New South Britain' by Captain William Smith in 1819, they quickly became known to British and US sealers (Stonehouse 2000), who successfully set about to deplete the islands' stock of fur seals and elephant seals. By the mid-19th century, little of either species was left, and to date, the remains of the sealers' camps may be found on the islands. During the early 20th century, the islands were also used as bases for whalers, until "inshore whaling died" (Stonehouse 2000, p. 115).

Since the International Geophysical Year (IGY, 1957-58), many nations have become interested in the South Shetland Islands, and **KING GEORGE ISLAND** (fig. 3-20) in particular has attracted a great number of stations for scientific research.

Figure 3-19: The Antarctic Peninsula and the Scotia Ridge. The Antarctic Peninsula, also called 'Antarctica's panhandle', and a number of islands are the remnants of an erstwhile land bridge between South America and Antarctica. From the southern tip of South America to the Antarctic Peninsula, South Georgia, South Sandwich Islands, South Orkney Islands, and South Shetland Islands mark the run of the Scotia Ridge. Circle (white arrow): King George Island.

Adapted from National Geographic Society (1971).

As Donachie (1994, p. 333) puts it, King George Island witnessed “a veritable stampede of construction workers” during the 1980s, and to date supports the research facilities of more than 10 nations (tab. 3-5).

King George Island, or Isla 25 de Mayo, as it is known to the Spanish-speaking world, is the largest of the South Shetland Islands. Approximately 95 % of the island is covered by an ice cap rising to 686 m. Some coastal areas are snow-free in the summer, and it is particularly in these areas that research stations have been set up. **Vegetation** cover is sparse, but rich by Antarctic standards, with lichens, mosses and the flowering plants *Colobanthus quitensis* and *Deschampsia antarctica* (Harris 1991a).

There are large populations of breeding wildlife on King George Island. Next to the three species of pygoscelid **penguins** (*P. adeliae*, Adélie; *P. papua*, Gentoo; *P. antarctica*, Chinstrap), other breeding **birds** mentioned in Peter & al. (1988), Harris (1991a), and Hahn & al. (1998) include Antarctic terns (*Sterna vittata*), Pintado or Cape petrels (*Daption capense*), Wilson’s storm petrels (*Oceanites oceanicus*), Southern giant petrels (*Macronectes giganteus*), Black-bellied storm petrels (*Fregetta tropica*), Dominican or Kelp gulls (*Larus dominicanus*), Imperial cormorants or Blue-eyed shags (*Phalacrocorax atriceps*), several species of skua (*Catharacta* spp.), and Greater sheathbills (*Chionis alba*). Breeding **mammals** listed in Harris (1991a) include Southern elephant seals (*Mirounga leonina*), Weddell seals (*Leptonychotes weddelli*), Crabeater seals (*Lobodon carcinophagus*), Leopard seals (*Hydrurga leptonyx*), and Antarctic fur seals (*Arctocephalus gazella*).

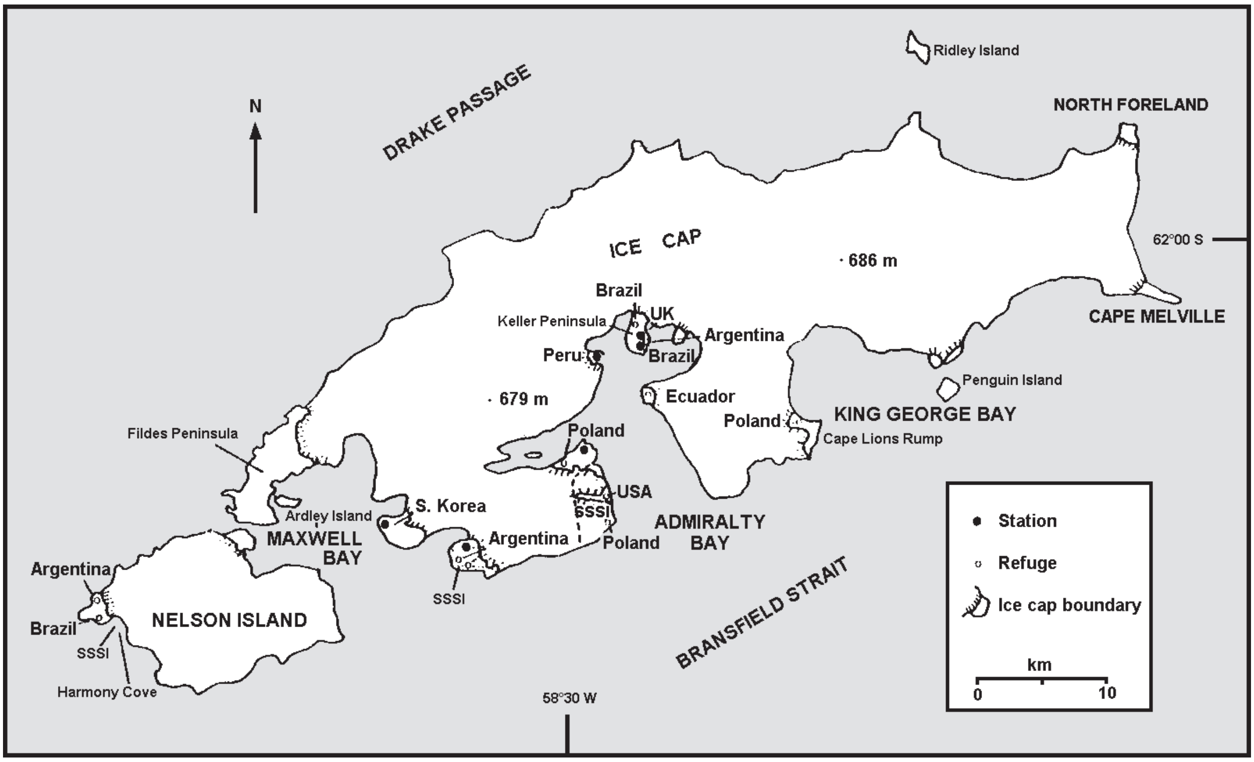

Figure 3-20: King George Island. King George Island is the largest of the South Shetland Islands. It is inhabited by numerous species of wildlife and also harbours a large number of research stations. From Harris (1991a)

In total, **nine research stations** and a number of summer-only refuges are currently in operation on the island (Table 3-5). King George Island has sometimes been called the ‘unofficial capital’ of Antarctica because of the numerous stations located there. According to White (1994, p. 255), “[t]he island seems overcrowded with potential environmental stress and – as of 1994 – over

12 km of gravel roads". WACE (1990, p. 331) considers King George Island the first "tourist resort in Antarctica", referring to the Chilean 'Teniente Rodolfo Marsh Martin'[59] base which sports a 'hotel' called 'Estrella Polar'[60]. HARRIS (1991b, p. 314) states that the nations represented on King George Island "share the management philosophy of the ATS, but different groups […] differ in approach."

On Keller Peninsula, Admiralty Bay, the UK station 'British Base G' (1947) was closed in 1961; it was later used intermittently by members of British Antarctic Survey (HARRIS 1991b). Stations are concentrated in Maxwell and Admiralty Bays (see fig. 3-20). The oldest research station still in use upon King George Island is '**Jubany**'. Supported and 'skeleton-staffed' by the Argentine military throughout the year, the number of inhabitants is significantly increased by scientists during the summer. In 1994, the German Alfred-Wegener-Institut für Polar- und Meeresforschung (AWI) established the '**Dallmann-Labor**', an annex station to Jubany Station named after the German explorer and polar researcher Eduard Dallmann (1830-1896). Apart from the commodious station and laboratory buildings, two refuges are maintained by the Argentines: Refugio Albatros and **Refugio Elefante**, the latter being close to the penguin colony studied for THIS THESIS. During two fieldwork seasons, I was based at Dallmann-Labor[61], and used Refugio Elefante as a convenient interim-stop on my way to the study colony.

Table 3-5: Research Stations and Refuges on King George Island, South Shetland Islands. Except for British Base G, stations are still operated. Stations are listed in alphabetical order of the nations maintaining them. Dates have been taken from HARRIS (1991a). * denotes a refuge

Name	Nationality	Established
Teniente Jubany[62]; Refugio Albatros*; Refugio Elefante*	Argentina	1948
Commandante Ferraz	Brazil	1984
Presidente Frei & Teniente Rodolfo Marsh Martin; Escudero*	Chile	1969, 1980
Great Wall	China	1985
Machu Picchu (summer-only)	Peru	1989
Henryk Arctowski	Poland	1977
Bellingshausen	Russia	1967/ 68
King Sejong	South Korea	1987
British Base G (closed in 1961)	UK	1947
Artigas	Uruguay	1985
Pieter J. Lenie, a.k.a. Copa Cabana (summer-only)	USA	1978

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[59] Teniente Marsh for short

[60] Polestar

[61] thanks to the hospitable spirit of the AWI

[62] Jubany for short

3.2.1 Location of Reconnaissance Field Work: SSSI[63] 8 (now ASPA[64] 128)

> “Western shore of Admiralty Bay, King George Island 62°11’S, 58°27’W. Approximate area: 17.5 km^2.
>
> An area on the western shore of Admiralty Bay, south of Ezcurra Inlet, south of a line connecting Jardine Peak and the shoreline immediately to the north of a prominent group of rocks characterized by a covering of orange lichens bearing approximately 068° from Jardine Peak, and east of a line joining Jardine Peak, The Tower and a point on the shoreline bearing 180° from The Tower. Designation on the grounds that the area supports an exceptional assemblage of Antarctic birds and mammals close to Arctowski Station (Poland), which is frequently visited by tourist ships. Long-term research programmes could be jeopardised by accidental disturbance, especially during the breeding season. Proposed by Poland. Adopted at the ATCM X (Washington, 1979). Designated for an indefinite[65] period.”

After Annex V of the Madrid Protocol on Environmental Protection entered into force, SSSI 8 (Western shore of Admiralty Bay) was renumbered and renamed, becoming ASPA 128. ASPA 128, in turn, is a part of the newly designated ASMA[66] Admiralty Bay.

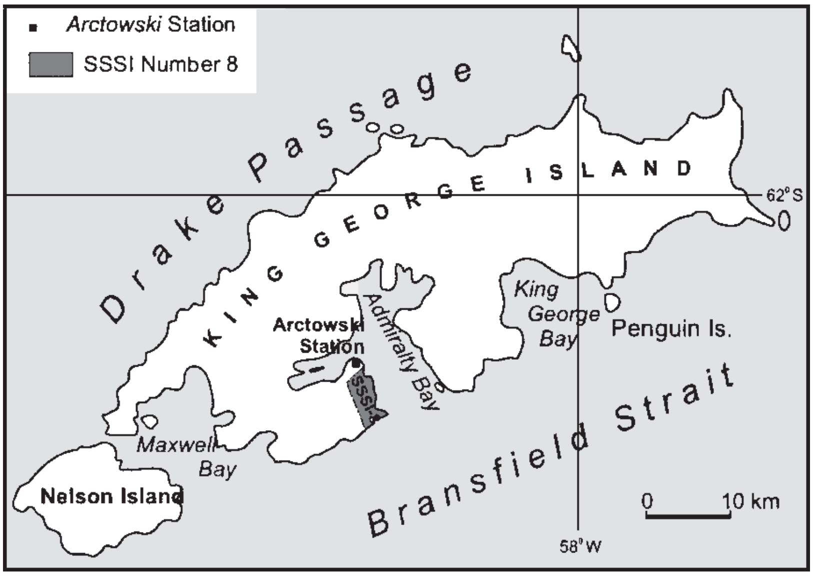

Figure 3-21: SSSI 8 (now ASPA 128). A preliminary field season was spent studying Adélie penguins and testing equipment at this location. From Pudełko (2003)

A preliminary ‘trial’ field season at SSSI 8/ ASPA 128 during November/ December 1999 served to test equipment and recording methods, and yielded data on behaviour and heart rate of unvisited penguins and penguins subjected to human visitation. As logistic intricacies necessitated a change in location, these data are not included in any of the analyses presented in this thesis. In accordance with ‘scientific lore’, however, they were used to gain a first-hand impression of Adélie penguin behaviour, test behaviour categories as well as equipment under field conditions, and formulate hypotheses (see Theoretical Background, section 2.4). For the preliminary field season, I was based at the Polish Station Henryk **Arctowski**.

---

[63] Site of Special Scientific Interest

[64] Antarctic Specially Protected Area

[65] Expiry of designation originally: 31 December 2000; later amended to designation for an indefinite period (Cohen (ed.) Handbook of the Antarctic Treaty System, 9th edition, 2002)

[66] Antarctic Specially Managed Area

3.2.2 Location of Study Site: SSSI 13 (now ASPA 132)

> “Potter Peninsula, ’25 de Mayo’ (King George) Island, South Shetland Islands 62°15’S, 58°39’W. Approximate area: 1.9 km^2.
>
> The site is on the east side of Maxwell Bay between ‘Mirounga Point’ and the east side of Stranger Point, and occupies the coastal zone of varying width up to 500m from the shoreline. Designation on the grounds that the area has a diverse avian and mammal fauna and locally rich vegetation. It is close to Jubany Station (Argentina) which is frequently visited by tour cruises. Long-term research programmes could be endangered by accidental disturbance, especially during breeding periods. Proposed by Argentina. Adopted at the ATCM XIII (Brussels, 1985). Designated for an indefinite period.”[67]

After Annex V of the Madrid Protocol on Environmental Protection entered into force, SSSI 13 (Potter Peninsula) was renumbered and renamed, becoming ASPA 132. The (idea to create a) revised management plan had already been adopted by Measure 3 at the XXIst ATCM (Christchurch 1997). A field visit to ASPA 132 carried out in January 2004 served as the basis for the revised management plan presented at the VIIth meeting[68] of the Committee of Environmental Protection (CEP) in Cape Town (2004) and accepted in 2005.

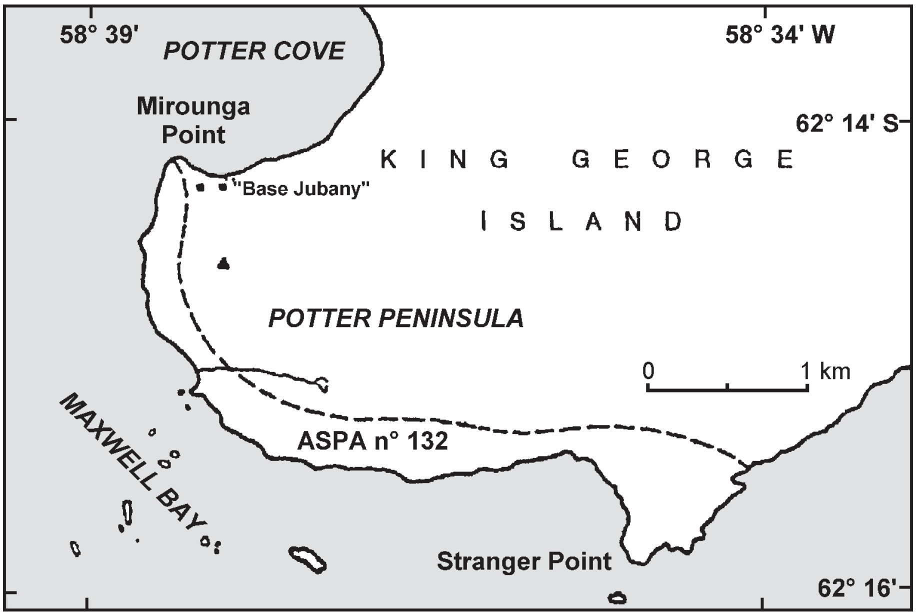

Figure 3-22: SSSI 13 (now ASPA 132). The study was conducted in the vicinity of Stranger Point. [source: aspire.nvi.net/DocImgWeb/SSSI13_13_8.tif]

At the time THIS STUDY took place, **entry** into SSSI 13 (fig. 3-22) required a **binational permit**, i.e. the German Umweltbundesamt and the Instituto Antartico Argentino (IAA) had to approve of the scientific research proposed. **Tourists** were not allowed to enter the area, and the **cruise ships** sighted during the time of THIS STUDY did not approach waters close to the penguins’ landing beaches. In both years, **scientific activities** included regular monitoring as well as one census of the smaller penguin sub-colonies, but not of the study sub-colony (see below). In addition to that, long-term research project on Elephant seals accounted for human presence (3-5 people) on the coastline and may have affected some[69] penguins returning to and leaving the sub-colony studied.

---

[67] http://cep.ats.aq/cep/apa/aspa/sites/aspa132/summary.html (acc.: 1 August 2010)

[68] The CEP meets annually in conjunction with the Antarctic Treaty Consultative Meeting (ATCM). With the agreement of the ATCM, however, there may be additional intersessional meetings if necessary.

[69] Penguins returned from different directions, not all of which led to beaches regularly frequented by scientists.

3.2.2.1 The Adélie Penguin Colony at Stranger Point

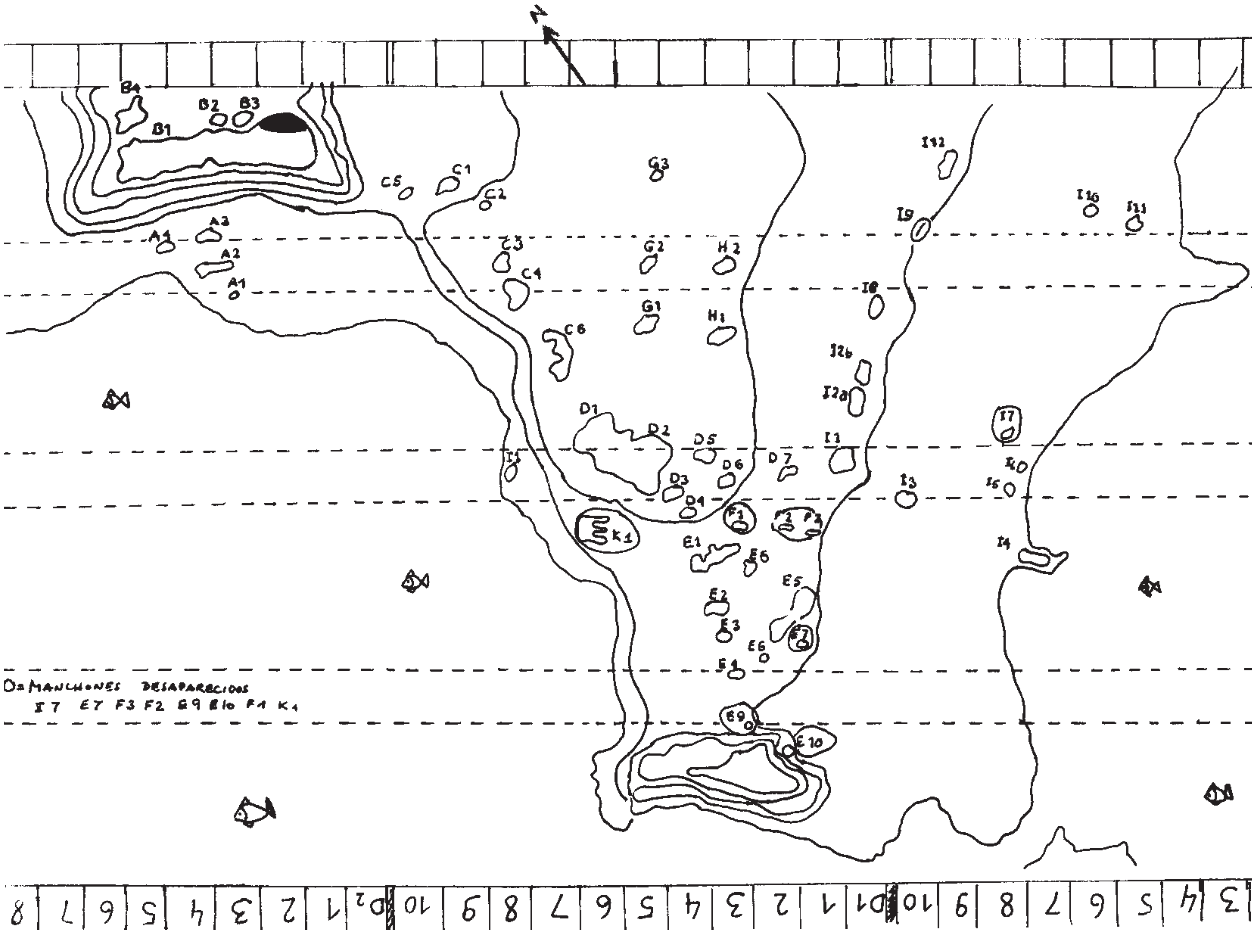

Figure 3-23: Schematic Drawing of the Adélie Penguin Colony at Stranger Point. The colony is divided into a number of sub-colonies. Approximately 50 % of the breeding pairs are found in the largest cluster of sub-colonies (PKC-B 1, 2, 3, 4). Black mark: location of study groups. Courtesy of PutiKlubCrew.

As seen in fig. 3-23, the Adélie penguin colony at Stranger Point is divided into a number of clustered sub-colonies.

N.b.: Even though sub-colonies have only been assigned capital letters and numbers in the drawing, the text shall add the prefix 'PKC' (short for PutiKlubCrew) to these sub-colony specifications to clearly distinguish them from the penguin groups (A, B, C, X, Y) studied.

The largest cluster of sub-colonies (PKC-B1, 2, 3, 4) holds roughly 50 % of the total number of breeding pairs (total colony: approx. 7,300 and 5,500 breeding pairs in 2000 and 2001, resp.). The penguin groups investigated in this study were situated at the north-eastern edge of sub-colony PKC-B1 (fig. 3-23, black mark).

Cluster PKC-B1, 2, 3, 4 is spread out across an elevated plateau, with a steep descent to a small stretch of coast to the south-southwest and an initially more gently ascending hill to the north-northeast approximately 25-30 m opposite the colony edge. The cluster is best accessed at the north-western edge, where a relatively narrow ascent exists between sub-colony PKC-B4 and the opposite hill (just outside the upper left corner of fig. 3-23). 'Hugging the slope of the hill' opposite the sub-colonies, the camouflaged observation tent (fig. 3-25) could be reached while keeping a maximum distance to incubating penguins.

3.2.2.2 Selection of Focal Groups and Focal Animals

A total of five groups of incubating Adélie penguins (*Pygoscelis adeliae*) were studied in two consecutive breeding seasons at SSSI 13 (now ASPA 132). Groups (2000: 3 groups, viz., A, B, C; 2001: 2 groups, viz., X, Y) were chosen from the largest cluster of Adélie sub-colonies (PKC-B 1, 2, 3, 4).

In this thesis, the term ‘**group**’ refers to an area of sub-colony rather than to a definite number of nests. During both field seasons, these areas, and thus the groups examined, were spaced between 15 m and 20 m apart for logistic reasons. For each group, the birds who received an artificial egg were termed **focal animals**. The nests chosen for focal-animal sampling differed between the years. On the video records, nests of focal animals were surrounded by a varying number of nests to the side and towards the centre of the colony; these constituted the **focal groups**.

The five groups examined (A, B, C: 2000; X, Y: 2001) were **not fully independent**: Groups B (fig. 3-24 **B**) and X (fig. 3-24 **X**) as well as groups C (fig. 3-24 **C**) and Y (fig. 3-24 **Y**) were located in roughly the same areas of the colony (see fig 3-24 **Overview**), with a partial **overlap** in area found between the former two (B, X), whereas areas of the latter two were **adjacent** (C, Y). The data obtained are thus definitely not spatially independent, but it is highly likely[70] that overall group composition was not identical. Situated uphill and not subjected to human visitation, group A (fig. 3-24 **A**) was only studied in the first field season and did not receive a corresponding group in the following.

A number of birds were chosen as **focal animals** in each of the five groups: two to four nests received artificial eggs to measure the incubating penguin’s heart rate (for details see chapter 4.1.2.1.1). Behaviour records were obtained from incubating penguins on all nests that held an artificial egg for any period of time.

In addition to studies on individual birds, **focal-group** analyses were performed on those nests situated in the first four rows of the colony that were captured on the video screen. They invariably included the focal animals.

Focal animals received an alphanumerical **identification code**, e.g. A5-1, in which the capital letter assigned the animal to one of the five groups, the first number identified the nest, and the second number coded the partner currently incubating. As for the latter, the number 1 indicated that the bird had been present during placement of the artificial egg (and had been paint-marked in the process).

Two nests received artificial eggs in mid-study, viz., B33 and C11. Nest numbers for these birds additionally kept record of the nest the artificial egg had originally been deployed in, i.e., nest number 33 coded for the fact that the egg had been transferred from nest number B3. Until the next change-over had been observed, the only distinction possible for these birds was prior-to- vs. after-egg-placement.

In a few instances, identification of breeders had not been possible due to ‘natural’ dirt marks obscuring the paint marks; these birds were labled ‘[group-nest-] 3’.

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[70] lack of individual markings does not permit a more conclusive phrasing

A (2000)

Y (2001)

Figure 3-24: Sub-Colonies PKC-B1 and PKC-B4, after the End of the First Field Season, December 2000, and Location of Study Groups within PKC-B1. PKC-B1 is the large, contiguous nesting area that contained the five study groups, while PKC-B4 constitutes the small separate cluster found at the lower right edge of 3-24 **Overview**. In 2000, group A (3-24 **A**) was situated about 10 m to the left and 5 m above from group B (3-24 **B**). Group C (3-24 **C**) was situated approximately 20 m to the right of group B. In 2001, a distance of about 20 m separated group X (3-24 **X**) from group Y (3-24 **Y**). Groups B (2000) and X (2001) were situated in overlapping areas, while groups C (2000) and Y (2001) were found in adjacent areas; for details, see text. © K.Schuster 2000, 2001

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3.2.2.3 Visitor Routes used for Visitation Experiments

For better comparison, **visitor routes** were identical in both seasons[71]: Stepping out of 'Castillo kiwi' (stonewall around tent), human visitors at groups B and X, respectively, approached the penguin colony more or less head-on in a straight line, while visitors at groups C and Y, respectively, walked along the foot of the hill opposite the colony until they had passed the group's sites, and then approached 'from the right' (from a visitor's point of view; fig. 3-25), again keeping the path straight. Stopping points at 15 m, 5 m and 3 m, respectively, were indicated by small piles of pebbles and rocks. To keep the respective distances to the focal birds, sideways movement was performed on a shallow parabola, with approximately equal extension to the left and right of the stopping points. Visitor retreat followed the same route but did not pause at any of the stopping points.

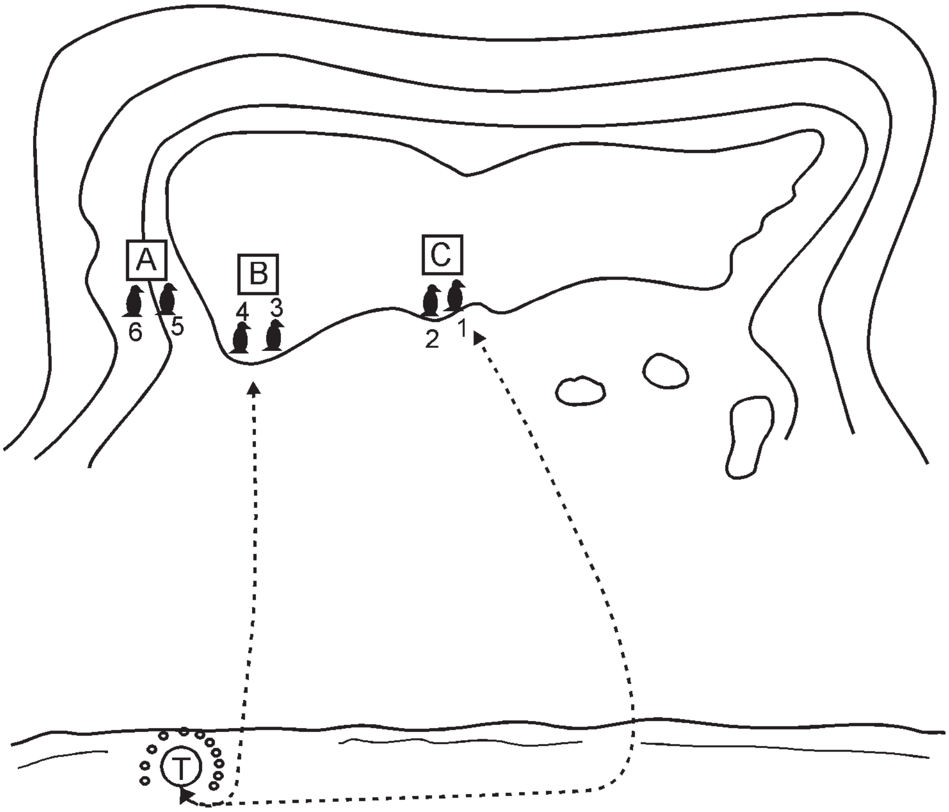

Figure 3-25: Visitor Routes used for Visitation Experiments. T: tent surrounded by stonewall; A, B, C: penguin groups; 1 to 6: focal nests. Arrows depict route taken by visitor.

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[71] Routes were kept, even though route B had been adopted to allow maximum distance from both other groups in 2000 – a feat rendered unnecessary in 2001 when no penguins were studied uphill.

4 Materials and Methods

After a trial field season at SSSI 8 (now ASPA[1] 128[2]; a Site of Special Scientific Interest situated near the Polish Antarctic Station Henryk Arctowski) in 1999, which predominantly served to test equipment, recording methods and visiting regimes, recordings for THIS STUDY were obtained at SSSI 13 (now ASPA 132[3]) in two consecutive years (2000, 2001) during the second halves of two incubation periods (mid- to end of November until the beginning of December). The respective maps are found in chapter 3, figs. 3-21 and 3-22.

To minimise bias due to observer impact, the study was designed to be predominantly hands-off. It was conducted on incubating penguins to facilitate distinction between the locomotory and the emotional component of heart rate changes (BLIX, STRØMME & URSIN 1974; BROOM & JOHNSON 2000) by keeping the former component to a minimum. To account for individual variation in resting heart rate as well as for susceptibility of heart rate to climatic conditions (cf. CULIK & al. 1989), each individual served as their own control (BALDOCK & SIBLY 1990).

4.1 Equipment

4.1.1 Behaviour/ Posture Data

For detailed behaviour recording, a **video camera** (Sony Handycam® Video Camera Recorder CCD-TR2000E Hi8/ PAL) was placed on a **tripod** out of sight of the penguins at a distance of approximately 25-30 m from the colony edge (fig. 4.1). Behaviour of the incubating penguins as well as of any conspecifics in the vicinity was recorded on **tape** (Hi8 video tapes, 90 min) and transcribed after the fieldwork periods. On the videos, the time of recording was shown in the bottom right corner. In addition to the electronic recording equipment, field **binoculars** (Leica, 8x20) and a field **scope** (Danubia Z-12; zoom: 12-36X50) were used for direct observations (e.g., identification and position of Focal-Animal nests to facilitate recognition during transcriptions). Direct observations were collected in a **field notebook**.

Figure 4-1: Behaviour Recording Equipment: The Video Camera. Behaviour of the penguins was filmed from inside a tent approx. 25-30 m away from the colony edge.

---

[1] Antarctic Specially Protected Area (q.v.)

[2] Admiralty Bay, King George Island (= Isla 25 de Mayo), South Shetland Islands, Maritime Antarctic

[3] Maxwell Bay, King George Island (= Isla 25 de Mayo), South Shetland Islands, Maritime Antarctic

4.1.2 Heart Rate Data

4.1.2.1 The Artificial Egg

The artificial eggs used in THIS STUDY were developed at Imperial College, London, and first employed by NIMON & al. (1994). They represent a technique for the non-invasive monitoring of heart rate in incubating penguins by use of an infrared sensor implanted in the egg rather than ‘planted onto’[4] the penguin themselves. The sensor makes contact with the incubating penguin’s highly vascularised brood patch and registers the pulse-varying volume of blood flow (fig. 4-2).

4.1.2.1.1 Construction Details

As described in NIMON & al. (1996), the **shell** of the artificial egg was originally modelled from a paper maché cast of a discarded Gentoo penguin (*Pygoscelis papua*) eggshell. To provide greater strength and waterproofing the paper surface was coated with three layers of fibreglass and epoxy resin. The finished egg (7.5 x 6 cm) was painted white (matt paint). Due to the smaller size of Adélie penguin eggs, the artificial eggs had to be downsized and repainted prior to employment in THIS STUDY.

The **infrared sensor** is mounted beneath a small transparent acrylic plastic window (1 cm in diameter) set in the long lateral side of the egg and flush with the surface. The sensor and its associated low-voltage electronic circuitry were housed in a plastic tube for ease of replacement. The tube is embedded in the egg interior, and the screened power/ signal cable leads out through the long side of the egg opposite to the sensor. At its outlet the cable is clamped with metal washers and epoxy resin. All components within the egg are sprayed with insulating lacquer. To achieve complete waterproofing and to provide both weight and further impact protection, the remaining space in the egg is filled with RTV[5] -sealant.

The cable leading to the egg is passed through a small wooden board (10 cm diameter) that sits immediately beneath the egg in the nest. This construction ensures that the egg maintains a **fixed orientation**, with the sensor facing up to the brood patch. The board and the base of the egg are buried in the gravel of the nest when the egg is implanted and the cable is passed through the nest’s wall. In this position, it does not affect the nesting penguin. In order to maintain a simple, robust system that would perform reliably in Antarctic conditions, **cable** was preferred over radio telemetry (e.g., HOWEY & al. 1984). To prevent inadvertent ensnarement of other penguins, the remainder of the cable is hidden underneath or between rocks.

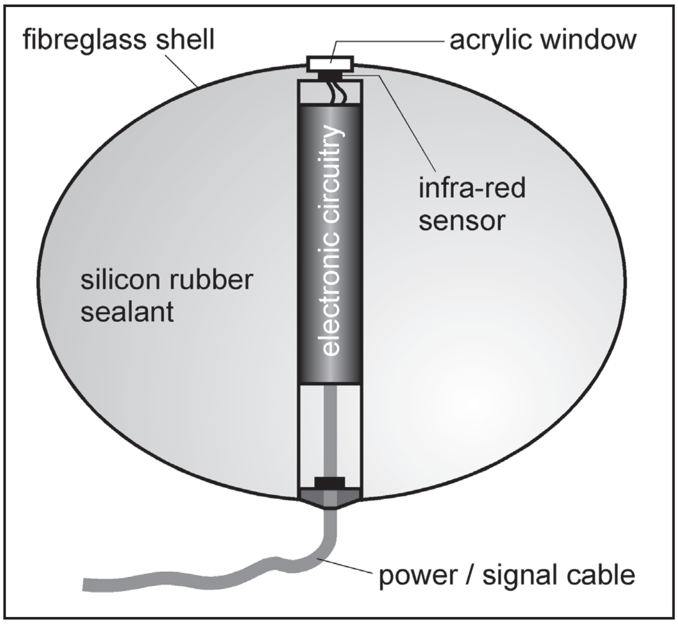

Figure 4-2: Heart Rate Recording Equipment I. Schematic construction of an artificial egg. Redrawn after NIMON (1997).

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[4] or inside

[5] RTV: short for room temperature vulcanising

The following facts continued to hold true for the eggs used in THIS STUDY. As the '& al.' in NIMON & al. (1996) comprised the developers of the artificial egg, the experts are quoted rather than rephrased.

> "The **infrared sensor** used to monitor heart rate was a UFI[6] photoelectric pulse transducer (model 1020) consisting of a matched emitter and photo resistor. When placed close to the skin of the pouch [= brood patch], the reflection of the infrared light was modulated by blood pulsing through the subcutaneous tissues. The modulation of light resulted in a small change in resistance of the photo resistor; this was monitored as a change in voltage that, when amplified, produced a high-level voltage output in the cable of approximately 1 volt peak to peak. The dynamic response characteristics of the sensor were far in excess of the cardiac pulsations. The sensor and associated electronics were powered by a remote **12-V battery supply**." (NIMON & al. 1996, p. 1020)

The modulation properties of the infrared beam are **sensitive to movement**: If the penguin remained prone (lying), movements such as shuffling (gently rocking on the egg to achieve a more comfortable position) or stretching, temporally distorted the record, while longer bouts of activity (getting up to manipulate eggs or to preen), produced longer passages of illegibility.

The **power/ signal cable** (length: 10 m) from each egg leads to a remote multiconnection box (which collects the signals of up to four eggs) and then, via a 50 m cable to the data logger. The purpose of the two **multiconnection boxes** used was to allow up to eight eggs to be monitored in parallel. Generally, heart rate of focal birds of the same group was monitored at the same time (two to three eggs in parallel). As the focal birds' behaviour was simultaneously videotaped, it was possible to relate these physiological responses with behaviour.

In some instances, heart rate from birds of groups not currently video-recorded was additionally monitored to acquire on-the-spot information on heart rate responses from more than one group (e.g., predator presence between two groups; response at 'never-visited' group A to visitation at other groups). These records were only accompanied by manually noted (un-taped) behavioural observations (ad lib.) and were not included in systematic analyses.

4.1.2.1.2 Placement Procedure

Placement procedure followed description in NIMON & al. (1996): A single person approached the nest slowly, remained an arm's length away and kept low to avoid 'looming' above the penguin[7]. The artificial egg was secured inside the penguin's nest by burying the platform and part of the height of the egg in the stones and gravel of the nest. The cable thus protruded through the wall. After reshaping the nest to its original position, the artificial egg resembled a natural penguin egg in the nest.

In THIS STUDY, placement of the artificial egg took on average 2.5 min. Even though the bird was free to leave the nest during placement, the majority of focal animals remained seated. Those who chose to get up stepped only a few metres away, and returned while the human intruder crouched quietly, enabling them to be **paint**-marked (water-based paint) with a long-handled **brush**. After a period of reconnaissance fieldwork in 1999 it became clear that blue markings were the only ones that stood any chance to stand out among the 'natural paint marks' the breeding birds quickly acquired in the course of their long stint of incubational occupation (these included any shades of

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[6] UFI Inc.: capital letters do not constitute an acronym; instrument-manufacturing company in California, USA

[7] … As FRID & DILL (2002, p. 11) put it: "Many animals initiate flight when the rate of change of angle subtended by an approaching object ('loom') exceeds some threshold."

yellow, orange, pink, red, purple, brown, green, and grey bordering on black). For video-recognition of the nests containing artificial eggs, the nest number was painted on a stone which was placed close to the nest.

4.1.2.1.3 Hardware and Software Requirements

As mentioned above, cables served to connect the artificial eggs with the data-storing device. A **data logger** (TTi[8] pod) was employed to feed the data stream recorded by the artificial eggs into a **laptop** (ASUS L8400). Two **spare laptop batteries** helped to counteract swift loss of battery power caused by low temperatures in the field. To power the artificial eggs, two **power stations** (Power Station, titan Autozubehör) were employed alternately.

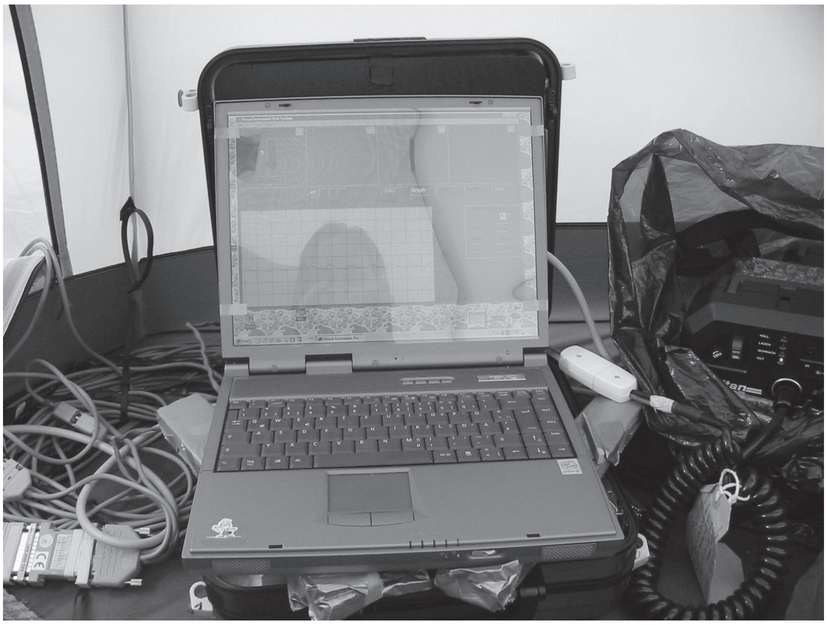

Figure 4-3: Heart Rate Recording Equipment II. Information collected in the artificial eggs was fed into the computer via a data logger. The software programme TTi VIPS enabled the observer to continuously monitor the quality of recordings. On the right hand side, the battery needed to power the artificial eggs is seen within its 'protective garment'.

The software programme **TTi VIPS** (Virtual Instrument Pod System, VIPS 203a) transformed the incoming data stream into voltage values. The data stream channelled through the logger was auto-saved in pre-numbered files (.prn- or .log-format) by the programme. The observer merely decided on the name of the first file, and determined the number of file-breaks. Saving one file and opening another every couple of minutes resulted in some intermittent data loss which, however, was accepted in favour of manageable file sizes. Recording rate varied between 8 data points (dp) per second (s^{-1}; i.e., one data point taken each 125 ms) and 100 dp s^{-1} (each 10 ms). On those occasions in 2000, during which a field assistant acted as visitor, recording rate was augmented to 200 dp s^{-1} (each 5 ms). Throughout the recording, heart rate was displayed on-screen for continuous monitoring (fig. 4-3). The lowest recording rate sufficed with respect to visualising heartbeats (fig. 4-4), but as the software had a tendency to infrequently omit one or more data points, it was considered prudent to increase data points per second.

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[8] TTi: Thurlby Thandar Instruments Ltd. in Cambridgeshire, UK

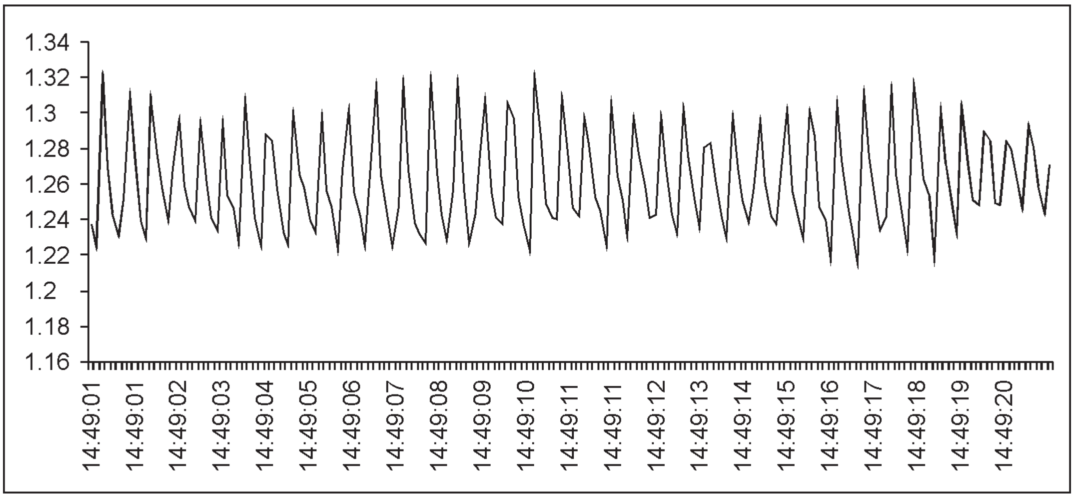

Figure 4-4: Heartbeats per 20 s as Depicted by a Recording Rate of 125 ms. The x-axis gives the time of recording, while the y-axis displays voltage. More data points per second traced the course of each heartbeat more closely.

4.1.3 Human Disturbance Data

For each visit, visitor number, behaviour and movements were written down in a **field notebook** or on pre-prepared sheets. To synchronise visitor data with behaviour and heart rate data, exact times (to the nearest second) were determined by a **digital wristwatch** checked against video and computer time prior to the beginning of each visit.

4.1.3.1 A Single Visitor

In the first field season in ASPA 132 (formerly SSSI 13; Potter Cove), the impact of a single visitor was examined. For eight visits (four each at groups B and C, respectively), another scientist volunteered to act as visitor. She/ He received detailed instructions as well as the procedure sheet (chronology of the visit in written form) prior to approaching the penguins. For the remainder of the time, there was no **field assistant** available; and the **observer** ‘doubled’ as visitor on these occasions.

4.1.3.2 The ‘Visiting Trio’

In the second field season in ASPA 132 (Potter Cove), the impact of a group of three visitors was examined. As it was unlikely that more than one (if any) field assistant(s) would be available at any time, **two artificial visitors** were created (fig. 4-5). The dummies were fastened to the frame of a dismantled backpack and could thus be carried by the ‘mobile visitor’ (observer).

4.1.4 Conspecific Disturbance Data

Data on conspecific disturbance were recorded on **video tape** (s.a., section 4.3.2).

4.1.5 Predator/ Aircraft Disturbance Data

Data on predator or aircraft disturbance were recorded on **video tape** (s.a., 4.3.2). Aircraft noise was additionally entered into the **field notebook**.

4.1.6 Weather Data

A total of six weather parameters were collected (s.b., section 4.2.7) with the following equipment: Wind speed and direction were measured by a hand-held **anemometer** which provided measurements in Beaufort, knots, and km h^{-1} (ANEMO, Fa. Deuta, Germany). Temperature at ground level and at 0.5 m above ground was taken with the help of a digital **thermometer** situated outside direct sunlight. Estimated cloud cover and precipitation were noted in a **field notebook**.

4.1.7 “My home is my castle”

A **stonewall**[1] which exceeded the average height of a standing Adélie penguin was constructed at the foot line of the hill opposite the study colony (at a distance of approximately 25-30 m) well before the beginning of the study (02.-04.11.2000). To shelter the equipment and hide the observer before, after, and between scheduled visits, a low **dome tent** (Tatonka) was erected within this stonewall (fig. 4-6). The stonewall concealed the lower half of the tent (thereby keeping visibility of opening/ closing movements to a minimum during camera employment) and kept out the worst gusts of wind (thereby helping to keep the tent in place).

Figure 4-5: The ‘Visiting Trio’. During the second field season at ASPA 132, impact of a group of three visitors was examined. Two dummies mounted onto the frame of a dismantled backpack were carried by the mobile visitor.

Figure 4-6: ‘Castillo kiwi’. A low dome tent within a stonewall served to shelter the equipment and hide the observer.

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9 aptly termed ‘castillo [= castle] kiwi’ by my Argentine colleagues

4.2 Data Collection

4.2.1 A Note on ‘Obstacles’ Encountered Prior to Data Collection at the Penguin Colony

4.2.1.1 Getting There – From Buenos Aires to Jubany Station/ Dallmann Laboratory

With the Dallmann Laboratory being annexed to Argentine (military) station Jubany, the German Alfred-Wegener Institute for Polar and Marine Research (AWI) holds a contract with the Argentine military permitting German scientists and personnel to travel on military airplanes between Buenos Aires (Argentina) and Jubany Station/ Dallmann Lab. Thanks to the courtesy of AWI, I was allowed to join their staff.

Flights start from Buenos Aires military airport, touch down for stopover and re-fuelling in Rio Gallegos (Southern Argentina), then fly on to Argentine station Marambio on Seymour Island (close to the tip of the Antarctic Peninsula). Marambio constitutes the regular location for a change of planes (from the long-distance ‘Hercules’ to the considerably smaller ‘Twin Otter’) and a distribution of military and scientific personnel, who take their posts on a number of stations and field camps. For the ‘Twin Otter’ to safely fly between Marambio and Jubany/ Dallmann Lab, however, acceptable weather conditions must simultaneously exist on both sides. Acceptability mainly refers to wind and sight, but also to temperature, since the landing strip at Jubany station is situated on a glacier. Moreover, the ‘Twin Otter’ can only carry a fraction of the original load of people and luggage destined for Jubany so that these acceptable weather conditions have to last for the duration of several flights.

Delays may occur in Buenos Aires[10] as well as at each stopover point. Whereas I was lucky as regards the first field season – with only a week spent at Marambio Station –, the second field season started considerably later than envisaged: Initially, the Argentine Military announced ‘a temporary fuel shortage’ which delayed the beginning of the campaign for close to two weeks. These were spent waiting in Buenos Aires. Following, scientists and station personnel alike were marooned on Marambio for nearly a fortnight facing inadequate weather conditions on one or both sides.

4.2.1.2 Getting There – From Jubany Station/ Dallmann Laboratory to the Penguin Colony

Based at Dallmann Laboratory, journeys to and from the penguin colony near Stranger Point were made on foot. The daily route depended on weather, tides, and ice conditions, and either took the form of an approximately 4 km walk along the coastline or a slightly shorter cross-country walk (see chapter 3, fig. 3-22). While the former included some scrambling over generally wet coastal rocks and necessitated the occasional avoidance of groups of sea elephants, the latter path led up and down ‘hills’ and skirted a lake the visibility of which improved as snow and ice receded. Technical equipment (computer, video camera, spare batteries) was carried back and forth, mainly to permit frequent recharging of batteries.

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[10] usually referred to as ‘una pequeña demora’ – a short delay – which to my experience may comprise anything from a day to over a fortnight

Climatic obstacles to fieldwork itself were generally linked to wind conditions and included storms, snowstorms, and rainstorms. On some occasions, reduced visibility during foggy weather kept people to the immediate surroundings of the station.

4.2.2 Behaviour/ Posture Data

Each day (weather permitting, s.a.), behaviour recordings on all **groups** investigated in that year were obtained in the morning (with recordings on the last group starting prior to 12 p.m.) and/or in the afternoon (with recordings on the first group starting later than 12 p.m.). In-between group recordings, there usually was a 5- to 10-minute delay, which was used for, e.g., repositioning of video camera, switching heart rate (q.v.) channels, or battery exchanges. In 2000 (three groups: A, B, and C, 18 behaviour recordings per group), each behaviour recording lasted 30 min (three groups per 90 min tape and day). In 2001 (two groups: X and Y, 14 and 12 behaviour recordings, respectively), each recording lasted 45 min[11] (two groups per 90 min tape). To compensate for the fact that the beginning of the second field season at ASPA 132 (formerly SSSI 13; Potter Cove) was considerably delayed (s.a.), more than one recording per group was obtained on most days.

In 2000, 27 h of taped behaviour/ posture data were collected on 18 days between 12 November and 04 December. In 2001, behaviour/ posture data were gathered for 20 h on 8 days between November 22 and December 02. Table 4-1 gives an overview of the behaviour recordings obtained per **group**.

Table 4-1: Numbers of Behaviour Recordings Collected on Video-Tape in Five Groups of Incubating Adélie Penguins during Two Consecutive Field Seasons. A, B, C, X, Y: study groups of penguins; 2000, 2001: year of data collection; no: no fieldwork possible for various reasons; vis: human visitation occurred; unvis: no human visitation occurred.

Behaviour recordings obtained per group; with (purple) and without (turquoise) human visitation																								
Day and Month / **Group (Year)**	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	**sum recordings per group**
A (2000)	1	1	1	no	1	1	no	1	1	1	no	1	1	1	1	1	1	1	no	1	1	no	1	**18**
B (2000) vis		1	1	no	1	1	no		1	1	no		1		1	1		1	no	1		no	1	**12**
B (2000) unvis	1			no			no	1			no	1		1			1		no		1	no		**6**
C (2000) vis		1	1	no	1	1	no		1	1	no		1		1	1		1	no	1		no	1	**12**
C (2000) unvis	1			no			no	1			no	1		1			1		no		1	no		**6**
X (2001) vis	2001: delayed arrival in the field											1	1		1	no		no	no	1	1	end of field-work		**5**
X (2001) unvis											2		1	2	1	no	0	no	no	1	2			**9**
Y (2001) vis												1	1		1	no		no	no	1	1			**5**
Y (2001) unvis											1		1	2	1	no	1	no	no	1				**7**
total behaviour recordings with human visitation: 34 (2000: 24; 2001: 10)																								
total behaviour recordings without human visitation: 46 (2000: 30; 2001: 16)																								

Within each group, a number of nests were chosen for Focal-Animal Sampling (see section 4.2.2.1), and table 4-2 lists the number of recordings per **focal animal**. In 2000, recordings yielded a total of 125 sessions (à 30 min) from 15 focal animals, while in 2001, a total of 70 sessions (à 45 min) were obtained from 10 focal animals.

Focal animals were **identified** by an alphanumerical code: A capital letter contained information on the group the animal belonged to (A, B, C, X, Y), the first number coded for the nest, while the

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[11] While the time schedule for human visitation remained the same, more time was spent recording penguin behaviour both before and after the visits.

second number specified whether the animal had been present (and marked) during placement of the artificial egg (-1) or not (-2). If the focal animal currently incubating could not be identified (e.g., markings not discernible due to dirt on or orientation of bird), the second number was noted as ‘-3’.

N.b.: Paint-marking the birds resident on the nest during placement of the artificial egg and thus distinguishing them from their naïve partners also permitted to examine differences displayed by a bird briefly disturbed during egg-deployment and their partner who had not encountered such disturbance. As preliminary analyses revealed substantial day-to-day variation in heart rate and behaviour of individuals (intra-individual), but did not detect consistent differences between birds that had or had not been present during placement of the artificial egg, this distinction is not referred to in analyses.

‘Baseline’ records of birds undisturbed by human visitation, and birds ‘naturally’ disturbed to varying degrees were obtained at regular intervals for all groups studied. ‘Regularity’ in this case refers to the schedule devised with respect to human visitation, while the term ‘naturally disturbed’ implies that no prior determination of occurrence or severity of disturbance was possible: While conspecifics were usually present, albeit at varying numbers, predators were encountered much more rarely.

‘Baseline’ records were used to assess the range of behaviours shown in the absence of human visitation, and to determine the background level of disturbance on top of which the additional human disturbance would occur. Details on human visitation are presented in the respective sections on disturbance.

4.2.2.1 Sampling and Recording Methods

> “When deciding on systematic rules for recording behaviour, two levels of decision must be made. The first, which we refer to as **sampling rules**, specifies which subjects to watch and when. The second, which we refer to as **recording rules**, specifies *how* the behaviour is recorded.” (MARTIN & BATESON 1993, p. 84)

In definitions of various sampling and recording methods suggested by different authors, these ‘three decisions on two levels’ (1.a whom and 1.b when, 2. how) frequently appear incompletely separated. In the following paragraphs, the terms Focal-Animal Sampling and Focal-Group Sampling (‘whom to watch’) are briefly characterised, followed by LEHNER’s (1998) comprehensive but rather ‘integrative’ definitions of sampling methods. Focusing primarily on the ‘when’ (the second of MARTIN & BATESON’s first-level decisions), LEHNER presents sampling methods as sub-categories of recording methods (MARTIN & BATESON’s second-level decision, i.e. ‘how’).

As the terms **state** and **event** come up in the following paragraphs, the difference is briefly recapitulated in box 4-1.

N.b.: In THIS THESIS, collection of behaviour data on video tapes was followed by two steps of data transcription: **Primary transcriptions** served to manually transfer taped information onto hard-copy matrices (sheets of paper), while **secondary transcriptions** involved entering data into the computer. Sampling and recording methods employed differed between these two steps. An overview of the sampling and recording methods used for each step is given in table 4-3.

Box 4-1: Recapitulation: States and Events.

States vs. Events

Most behaviours can be divided into two categories based on their **relative duration** (Altmann 1974; Lehner 1998):

State: An ongoing behaviour; a behaviour that can be timed with a stopwatch (e.g., resting). Postures[12] ('prone', 'up') likewise constitute states (but see footnote).

Event: A momentary behaviour; a behaviour that happens so suddenly and/or fast that only its occurrence can be meaningfully recorded (e.g., headshakes). A change between states may also constitute an event (e.g., for flying birds: the take-off between sitting/ perching and flying).

4.2.2.1.1 Focal-Animal and Focal-Group Sampling[13]

Following the terminology of Martin & Bateson (1993, p. 84; s.a.), the terms Focal-Animal Sampling and Focal-Group Sampling predominantly refer to the first of the first-level decisions ('whom to watch').

In **Focal-Group Sampling**, an entire group is in the focus of observations.

In **Focal-Animal Sampling**, a single individual is chosen, and their behaviour is in the focus of observations. In case of social/ agonistic interactions, these observations may or may not include the animal(s) interacting with the focal animal.

Although, to some extent, the choice of (number of) focal subjects determines the nature of the data collected as regards the 'when' and 'how', Martin & Bateson (1993, p. 85) stress that "any of the three different recording methods (Continuous Recording, Instantaneous Sampling or One-Zero Sampling) can be used when recording the behaviour of a single animal".

4.2.2.1.2 Continuous Recording Sampling Method

Continuous Recording Sampling Methods (Lehner 1998) are used to record a complete account of all behaviour units of interest; i.e. data on occurrence, duration and sequences of both states and events are obtained. These sampling methods provide the most complete and accurate data. In the field, they are usually only feasible when a limited number of behaviours are observed in a single individual (i.e., Focal-Animal Sampling; but see below).

All-Occurrences Sampling (Lehner 1998; in this thesis abbreviated to AOS) is one of the sampling methods subsumed under Continuous Recording. It serves to record all occurrences of a particular behaviour. According to Lehner (1998, p. 197), All-Occurrences Sampling of selected behaviours is possible if the following conditions apply:

1. The animals and the behaviours are easily observed.
2. The behaviours have been carefully defined so that they are easily recognised.
3. The behaviours do not occur more often (or more rapidly) than the observer can record them.

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[12] Strictly speaking, posture constitutes a behaviour state as well. Given the fact, however, that the penguin is able to perform a great number of behaviours either while prone or while sitting/ standing, posture was considered a separate category.

[13] also referred to as 'Focal Sampling' (Martin & Bateson 1993)

Table 4-2: Numbers of Behaviour Recordings of <u>Focal Animals</u> Collected on Video-Tape in Five Groups of Incubating Adélie Penguins during Two Consecutive Field Seasons. Focal animals were 'named' alphanumerically, with A, B, C, X, Y representing the study groups, the first number referring to the nest and the second one to the bird currently incubating. 2000, 2001: year of data collection; FA: focal animal; no: no fieldwork possible for various reasons; [group-nest]-3: unidentified incubator; vis: human visitation occurred; unvis: no human visitation occurred. (page 1 of 2)

Behaviour recordings obtained per Focal Animal (FA); with (purple) and without (turquoise) human visitation

Day and Month / FA (year)	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	sum recordings obtained per FA
A5-1 (2000) unvis				no	1	1	no	1	1	1	no	1	1	1	1	1			no			no		**10**
A5-2 (2000) unvis				no			no				no						1	1	no	1	1	no	1	**5**
A5-3 (2000) unvis	1	1	1	no			no				no								no			no		**(3)**
A6-1 (2000) unvis		1		no			no	1	1	1	no	1	1						no	1	1	no	1	**9**
A6-2 (2000) unvis			1	no	1	1	no				no			1	1				no			no		**5**
A6-3 (2000) unvis	1			no			no				no					1	1	1	no			no		**(4)**
B3-1 (2000) vis		1		no			no				no		1		1				no			no		**3**
B3-1 (2000) unvis	1			no			no				no			1					no			no		**2**
B3-2 (2000) vis			1	no	1	1	no		1	1	no								no			no		**5**
B3-2 (2000) unvis				no			no	1			no	1							no			no		**2**
B3-3 (2000) vis				no			no				no					1		1	no	1		no	1	**(4)**
B3-3 (2000) unvis				no			no				no						1		no		1	no		**(2)**
B4-1 (2000) vis		1	1	no	1	1	no		1	1	no								no			no		**6**
B4-1 (2000) unvis	1			no			no	1			no								no			no		**2**
B4-2 (2000) vis				no			no				no		1		1	1		1	no	1		no	1	**6**
B4-2 (2000) unvis				no			no				no	1		1			1		no		1	no		**4**
B33-1 (2000) vis				no			no				no							1	no	1		no	1	**3**
B33-1 (2000) unvis				no			no				no						1		no		1	no		**2**
B33-2 (2000) vis		1	1	no	1	1	no		1	1	no		1		1	1			no			no		**9**
B33-2 (2000) unvis	1			no			no	1			no	1		1					no			no		**4**
C1-1 (2000) vis		1	1	no	1	1	no		1	1	no		1		1				no			no		**8**
C1-1 (2000) unvis	1			no			no	1			no	1		1					no			no		**4**
C1-3 (2000) vis				no			no				no					1		1	no	1		no	1	**(4)**
C1-3 (2000) unvis				no			no				no						1		no		1	no		**(2)**
C2-1 (2000) vis		1	1	no	1		no				no							1	no	1		no	1	**6**
C2-1 (2000) unvis	1			no			no				no						1		no		1	no		**3**
C2-2 (2000) vis				no		1	no		1	1	no		1		1	1			no			no		**6**
C2-2 (2000) unvis				no			no	1			no	1		1					no			no		**3**
C11-1 (2000) vis				no			no				no				1	1		1	no	1		no	1	**5**
C11-1 (2000) unvis				no			no				no						1		no		1	no		**2**
C11-2 (2000) vis		1	1	no	1	1	no		1	1	no		1						no			no		**7**
C11-2 (2000) unvis	1			no			no	1			no	1		1					no			no		**4**

Table 4-2: Numbers of Behaviour Recordings of Focal Animals Collected on Video-Tape in Five Groups of Incubating Adélie Penguins during Two Consecutive Field Seasons. (page 2 of 2)

Behaviour recordings obtained per Focal Animal (FA); with (purple) and without (turquoise) human visitation																								
Day and Month / **FA (year)**	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	**sum recordings obtained per FA**
X1-1 (2001) vis	2001: delayed arrival in the field											1	1		1	no		no	no			end of field-work		**3**
X1-1 (2001) unvis											2		1	2		no		no	no					**5**
X2-1 (2001) vis												1	1		1	no		no	no					**3**
X2-1 (2001) unvis											2		1	2	1	no		no	no					**6**
X2-2 (2001) vis																no		no	no	1	1			**2**
X2-2 (2001) unvis																no	1	no	no	1	2			**4**
X3-1 (2001) vis												1	1			no		no	no					**2**
X3-1 (2001) unvis											2		1			no		no	no					**3**
X3-2 (2001) vis															1	no		no	no	1	1			**3**
X3-2 (2001) unvis														2	1	no	1	no	no	1	2			**7**
Y4-1 (2001) vis												1	1		1	no		no	no					**3**
Y4-1 (2001) unvis											1		1	2	1	no		no	no					**5**
Y5-1 (2001) vis												1	1		1	no		no	no					**3**
Y5-1 (2001) unvis											1		1	2	1	no		no	no					**5**
Y5-2 (2001) vis																no		no	no	1	1			**2**
Y5-2 (2001) unvis																no	1	no	no	1				**2**
Y6-1 (2001) vis												1	1			no		no	no					**2**
Y6-1 (2001) unvis											1		1	2		no		no	no					**4**
Y6-2 (2001) vis															1	no		no	no	1	1			**3**
Y6-2 (2001) unvis															1	no	1	no	no	1				**3**
total sessions recorded of identifiable FAs: 195 (A: 29; B: 48; C: 48; X: 38; Y: 32)																								

This method of sampling can provide accurate data on the following:

1. Frequency[13] and rate[14] of occurrence (and temporal changes in rate) of the selected behaviours.
2. Restricted sequencing[15].
3. Behavioural synchrony[16].

As for the video recordings obtained in THIS STUDY, the possibility to replay sequences if necessary made it possible to expand the number of behaviours and to transcribe and subsequently compare the behaviour of several individuals with respect to the same period of time. Of the examples listed above, only frequency and rate were relevant to THIS STUDY.

Focal-Group All-Occurrences Sampling was employed in the primary transcription (video data onto paper) of a selected behaviour event (headshakes) in the absence/ presence of one or three human visitors. For each 30 s sampling interval, frequency of headshakes was noted chronologically and individually, identifying the respective bird by nest location (for details s.b., section 4.3.2.3).

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[13] i.e., number of occurrences (absolute frequency) or proportion of occurrences (relative frequency)

[14] i.e., frequency per time unit (e.g., number of occurrences per 30 s-interval)

[15] not applicable to THIS STUDY

[16] not applicable to THIS STUDY

Focal-Animal All-Occurrences Sampling was used in the primary transcription of focal-animal behaviour. The individual's posture, their position relative to the camera angle and all behaviour elements were noted second by second. Numbers, movements and selected behaviours of stationary and passing conspecifics in the vicinity of the focal animal were likewise transcribed that way.

By allocating behaviour elements to behaviour systems, All-Occurrences Sampling was also used to gain information on distribution of behaviour systems within a session (behavioural topography, q.v.).

4.2.2.1.3 Time[17] -Sampling Methods

Lehner (1998, p. 201f.) distinguishes two main sampling methods within Time Sampling.

Using **Instantaneous/ Scan Sampling**[18], the observer scores an animal's behaviour (or the behaviours of several animals) at predetermined 'points' in time, whereas **One-Zero Sampling**[19] serves to record whether a behaviour state – or, less frequently, event – occurred (one) or did not occur (zero) during a sample interval delineated by points in time.

According to Lehner (1998, p. 202), these methods are often used under the following conditions:

1. To gather data on a few behaviours while simultaneously sampling a relatively large group of individuals (e.g. studies of behavioural synchrony; daily activity patterns; percentage of time spent in behaviours of specific interest).
2. To gather data on a larger number of behaviours on a few individuals (e.g. juvenile females), than we can with continuous sampling methods (e.g. time budgets for an exhaustive list of mutually exclusive behaviours).
3. To maintain a high inter-observer reliability when several observers with varying levels of ability and experience are by necessity involved gathering data[20].

4.2.2.1.4 Instantaneous-Scan Sampling

> "Instantaneous Sampling can be used to obtain data from a large number of group members by observing each in turn. Moreover, if the behavior [sic] of all visible group (or subgroup) members are [sic] sampled within a very short time period the record approaches a simultaneous sample on all individuals." (Altmann 1974, p. 258f.)

The major benefit of Instantaneous-Scan Sampling[21] is the relative ease of recording data versus All-Occurrences Sampling. According to Lehner (1998, p. 205), this method works well with behaviour states but is not recommended for use with events.

Focal-Group Instantaneous-Scan Sampling (ISS) was used to gather data on behaviour states and posture (prone, i.e. lying down, vs. sitting or standing) of groups of penguins in the absence/

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[17] The full term should by right of categorisational consistency read 'Time Recording Sampling Methods', as the term time refers to a way of recording ('from time to time' as opposed to 'continuous'), rather than to a way of sampling.

[18] also termed 'time-sampling', (Hutt & Hutt 1970), 'point sampling' (Dunbar 1976), or 'on-the-dot sampling' (Slater 1978)

[19] also termed 'time-sampling' (Hutt & Hutt 1970), or 'Hansen system' (Fienberg 1972 quoted in Lehner 1998)

[20] not applicable to this study

[21] To emphasise that the data presented in this study represent 'truly instantaneous' samples for the entire group, the sampling method will be referred to as Instantaneous-Scan Sampling.

presence of one or three human visitors. Additionally, the numbers of **conspecifics** present inside the group or in its vicinity were transcribed.

With respect to **focal animals**, this method was not employed.

4.2.2.1.5 One-Zero Sampling

Focal-Group One-Zero Sampling (OZS, Altmann 1974) was used in secondary transcriptions to render focal-group data originally transcribed using All-Occurrences Sampling (behaviour event: headshakes) compatible to the information obtained by Instantaneous-Scan Sampling for the same groups. One-Zero Sampling consisted of noting for each individual within the focal group, whether they had or had not performed at least one headshake per 30 s interval. This method was at this stage considered to yield more appropriate results, as it directly reflected the number of penguins reacting, rather than representing a mixture of ‘more penguins’ and ‘the same penguin more often’.

With respect to **focal animals**, this method was not employed.

4.2.2.1.6 Not quite a Sampling ‘Method’: Ad Libitum Sampling

> “With Ad Lib. Sampling, it is rarely possible to determine which differences in data are due to true differences between individuals, age-sex classes, or behaviors [sic], and which due merely to biases in sampling. […] In any field study, some data probably will consist of such records, which may be of considerable use as illustrative material and because of their heuristic value in searching for ideas and in planning systematic sampling of behavior. Often, too, rare but significant events are recorded during such non-systematic sampling periods.” (Altmann 1974, p. 236f.)

In this study, Ad Libitum Sampling was not used to obtain data on the behaviour of the study birds themselves but employed to additionally record inordinary and/ or infrequent events which occurred in the vicinity of (or in the air above) the study birds and which were considered likely to have a potential impact on the birds’ behaviour and/ or heart rate.

Table 4-3: Overview of Sampling and Recording Methods Used in This Study. I: primary data transcription (video data into hard-copy matrix); II: secondary data tanscription (hard-copy matrix into Excel/ SPSS spreadsheets).

Sampling Method	Choice of Subjects	Usage in this Study
Continuous Recording Sampling Method Lehner (1998)	Focal Groups, Focal Animals	Data collection in the field (behaviour)
1. All-Occurrences Sampling	Focal Groups	Data transcription I: behaviour event – headshakes
	Focal Animals	Data transcription I: posture, behaviour elements, conspecifics (number, behaviour, velocity of movement)
	Focal Animals	Data transcription I: behaviour systems
Time Sampling Methods Lehner (1998)	Focal Groups	Data transcriptions
1. Instantaneous-Scan Sampling	Focal Groups	Data transcriptions I and II: posture, behaviour states, conspecifics (number)
2. One-Zero Sampling	Focal Groups	Data transcription II: behaviour event – headshakes
Ad Lib. Sampling Altmann (1974)	opportunistic/ non-specific	Documentation of unusual or infrequent events/ disturbances

Records included, for example, **fights** between neighbours, fights between neighbours and conspecific ‘visitors’, nest **attacks** by skuas (*Catharacta* spp.), low, medium and high **overflights** by skuas or Southern giant petrels (*Macronectes giganteus*), passing **congeners** (Gentoos, *Pygoscelis papua*, or Chinstraps, *P. antarctica*), aircraft **noises** resulting from helicopters or planes, and noises accidentally emanating from the observer’s hiding place[22]. Abrupt **climatic** changes, such as the onset of heavy snowfall were likewise noted.

4.2.3 Heart Rate Data

> “The system used to monitor the heart rate must not itself have an effect on the animal.”
> (Broom & Johnson 2000, p. 92)

Heart rate was measured using artificial eggs fitted with infra-red sensors (q.v. section 4.1.2.1, fig. 4-2). For this study, a total of **six artificial eggs** were available in each season. Within each group examined, two (2000: A, B, C) or three (2001: X, Y) nests were simultaneously fitted with artificial eggs; and heart rate data of those penguins were generally obtained at the same time as the video recordings on the entire group. Although the bird resident at the time of egg insertion had been paint-marked, these markings were not always readily identifiable. Heart rate data from ‘unidentified incubators’ were not included in the analyses of differences between individual focal animals (table 4-4). In some cases, heart rate recordings from identified focal animals were available without transcribable behaviour records to match them[23]. This was most often the case when a focal animal had persistently turned its back to the camera, and differentiation between different behaviour elements was rendered impossible. Such records were exclusively used in preliminary analyses (e.g., in the elusive quest for ‘average’ HR in individual FAs), but not included in the analyses ‘proper’.

During the first field season at ASPA 132, it was in some cases necessary (and possible) to translocate one of the artificial eggs within the group so that for group B, heart rate records were obtained from five instead of four birds (viz., twice both partners of the nests originally supplied, plus one extra bird), while for group C, records were gathered from six birds (of which one of the original birds, C1-2, failed to pass transcription). Due to the severely shortened fieldwork period, this was not feasible in 2001. Moreover, in each of the two groups examined during that season there was one nest, for which heart rate of only one of the two partners could be recorded (X1-1, Y4-1), because the respective partners refused to accept the artificial egg. Table 4-4 gives an overview of the heart rate records collected per focal animal.

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[22] e.g., removal of a heavy load of snow from the roof of the tent

[23] e.g., B3-3, 23.11.2000 – a session without human visitation

Table 4-4: **Numbers of Heart Rate Recordings of Focal Animals in Five Groups of Incubating Adélie Penguins during Two Consecutive Field Seasons.** Focal animals were ‘named’ alphanumerically, with A, B, C, X, Y representing the study groups, the first number referring to the nest and the second one to the bird currently incubating. 2000, 2001: year of data collection; FA: focal animal; no: no fieldwork possible for various reasons; [group-nest]-3: unidentified incubator; vis: human visitation occurred; unvis: no human visitation occurred. Note that visiting schedule has been marked even for birds not currently supplied with an artificial egg. (page 1 of 2)

Heart rate recordings obtained per FA; from sessions with (purple) and without (turquoise) human visitation obtained per FA																							
Day and Month / Group (Year)	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	sum re-cordings obtained per FA
A5-1 (2000) unvis				no	1	1	no	1	1	1	no	1	1	1	1	1			no			no		**10**
A5-2 (2000) unvis				no			no				no						1	1	no	1	1	no	1	**5**
A5-3 (2000) unvis	1	1	1	no			no				no								no			no		**(3)**
A6-1 (2000) unvis		1		no			no	1	1	1	no	1	1						no	1	1	no	1	**9**
A6-2 (2000) unvis			1	no	1	1	no				no			1	1				no			no		**5**
A6-3 (2000) unvis	1			no			no				no					1	1	1	no			no		**(4)**
B3-1 (2000) vis		1		no			no				no		1		1				no			no		**3**
B3-1 (2000) unvis	1			no			no				no			1					no			no		**2**
B3-2 (2000) vis			1	no	1	1	no		1	1	no								no			no		**5**
B3-2 (2000) unvis				no			no	1			no	1							no			no		**2**
B3-3 (2000) vis				no			no				no					1		1	no	1		no	1	**(4)**
B3-3 (2000) unvis				no			no				no						1		no		1	no		**(2)**
B4-1 (2000) vis		1	1	no	1	1	no		1	1	no								no			no		**6**
B4-1 (2000) unvis	1			no			no	1			no								no			no		**2**
B4-2 (2000) vis				no			no				no		1		1	1		1	no	1		no	1	**6**
B4-2 (2000) unvis				no			no				no	1		1			1		no		1	no		**4**
B33-1 (2000) vis				no			no				no							1	no	1		no	1	**3**
B33-1 (2000) unvis				no			no				no						1		no		1	no		**2**
B33-2 (2000) vis		🟪	🟪	no	🟪	🟪	no		🟪	🟪	no		🟪		🟪	🟪			no			no		**no egg**
B33-2 (2000) unvis	🟦			no			no	🟦			no	🟦		🟦					no			no		**no egg**
C1-1 (2000) vis		1	1	no	1	1	no		1	1	no		1		🟪				no			no		**7**
C1-1 (2000) unvis	1			no			no	1			no	1		1					no			no		**4**
C1-3 (2000) vis				no			no				no					🟪		🟪	no	🟪		no	🟪	**no egg**
C1-3 (2000) unvis				no			no				no								no			no		**no egg**
C2-1 (2000) vis		1	1	no	1		no				no							1	no	1		no	1	**6**
C2-1 (2000) unvis	1			no			no				no						1		no		1	no		**3**
C2-2 (2000) vis				no		1	no		1	1	no		1		1	1			no			no		**6**
C2-2 (2000) unvis				no			no	1			no	1		1					no			no		**3**
C11-1 (2000) vis				no			no				no				1	1		1	no	1		no	1	**5**
C11-1 (2000) unvis				no			no				no						1		no		1	no		**2**
C11-2 (2000) vis		🟪	🟪	no	🟪	🟪	no		🟪	🟪	no		🟪						no			no		**no egg**
C11-2 (2000) unvis	🟦			no			no	🟦			no	🟦		🟦					no			no		**no egg**

Table 4-4: **Numbers of Heart Rate Recordings of Focal Animals in Five Groups of Incubating Adélie Penguins during Two Consecutive Field Seasons.** (page 2 of 2)

Heart rate recordings obtained per FA; from sessions with (purple) and without (turquoise) human visitation obtained per FA

Day and Month / Group (Year)	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	sum re-cordings obtained per FA
X1-1 (2001) vis	2001: delayed arrival in the field											1	1		1	no		no	no			end of field-work		**3**
X1-1 (2001) unvis											2		1	2	1	no		no	no					**6**
X2-1 (2001) vis												1	1		1	no		no	no					**3**
X2-1 (2001) unvis											2		1	2	1	no		no	no					**6**
X2-2 (2001) vis																no		no	no	1	1			**2**
X2-2 (2001) unvis																no	1	no	no	1	2			**4**
X3-1 (2001) vis												1	1			no		no	no					**2**
X3-1 (2001) unvis											2		1			no		no	no					**3**
X3-2 (2001) vis															1	no		no	no	1	1			**3**
X3-2 (2001) unvis														2	1	no	1	no	no	1	2			**7**
Y4-1 (2001) vis												1	1		1	no		no	no					**3**
Y4-1 (2001) unvis											1		1	2	1	no		no	no					**5**
Y5-1 (2001) vis												1	1		1	no		no	no					**3**
Y5-1 (2001) unvis											1		1	2	1	no		no	no					**5**
Y5-2 (2001) vis																no		no	no	1	1			**2**
Y5-2 (2001) unvis																no	1	no	no	1				**2**
Y6-1 (2001) vis												1	1			no		no	no					**2**
Y6-1 (2001) unvis											1		1	2		no		no	no					**4**
Y6-2 (2001) vis															1	no		no	no	1	1			**3**
Y6-2 (2001) unvis															1	no	1	no	no	1				**3**

total HR-sessions recorded: 171 (2000: 100; 2001: 71); total number of FAs (excluding unidentified birds): 23 (13+10)

4.2.4 Human Disturbance Data

Recapitulation: Data on human visitation were not collected on video tape; instead, **field notebook** entries contained exact times (to the nearest second) and locations which were matched with video (behaviour, conspecifics, predators/ aircraft) and computer-logged data (heart rate) during transcriptions.

Visits were conducted at four of the five groups studied (2000: B, C; 2001: X, Y). Group A (2000) was not subjected to any human contact between placement and extraction of the artificial eggs. In the other four groups, visits were scheduled to take place on two out of three days[24] (purple cells in tables for behaviour/ heart rate recordings above). **Visitor routes** in relation to location of groups have been illustrated in chapter 3 (fig. 3-25). The **four** different **visiting regimes** followed the same time schedule. Detailed information on the **visiting experiments** is found in section 4.3.4.2.

4.2.5 Conspecific Disturbance Data

Given the proceedings of daily life within a penguin colony, data on conspecific disturbance were recorded simultaneously with those of the five study groups (same tape).

4.2.6 Predator/ Aircraft Disturbance Data

Data on predator or aircraft presence were ‘collected’ together with behaviour and posture of focal animals on the same video tape.

Due to focus on the colony, i.e., on the ground, accounts of **airborne** predator presence must be considered incomplete: The majority of medium and high overflights were at best captured as shadows passing over the incubating birds. In contrast, records of predator presence on the **ground** as well as those of low overflights are representative of actual occurrences. **Aircraft** noise could be heard inside the tent; it was additionally entered into the field notebook.

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[24] The remaining days served to collect behaviour and heart rate data on entirely undisturbed birds and on ‘naturally’ disturbed birds (e.g., by conspecifics, predators, aircraft noise).

4.2.7 Weather Data

Six weather parameters were sampled at the beginning and end[25] of each recording bout, i.e., before and after all of the sessions:

- wind speed (in km h^{-1}), if applicable including notes on presence and severity of gusts,
- wind direction,
- ground temperature (°C),
- temperature at 0.5 m above ground (°C),
- cloud cover (0 %, 25 %, 50 %, 75 %, and 100 %), and
- precipitation (none, rain, sleet, snow).

If morning and afternoon recording bouts occurred on the same day, weather parameters were taken separately for each:

Tables 4-5 and 4-6 provide an overview of weather data collected per day for each year.

Table 4-5: Weather Data Collected – 2000. arr: arrival at tent, dep: departure from tent; temp: temperature; min.: minimum, max.: maximum, mean: mean from min.&max.; gusts: abrupt increases in wind speed; missdat: data missing. (page 1 of 2)

Arrival date	**visit/ baseline**	**time arr**	**temp (°C) ground arr**	**temp (°C) 0.5m arr**	**wind-speed (km/ h) min. arr**	**wind-speed (km/ h) max. arr**	**mean wind-speed (km/ h) arr**	**wind-gusts (km/ h) arr**	**wind-direction arr**	**cloud-cover (%) arr**	**precipitation arr; 0=none LS=light snow S=snow R=rain; Dr=drizzle**
12.11.2000	b	13:50	2.0	not yet obt.	not yet obt.	not yet obt.	not yet obt.	not yet obt.	not yet obt.	not yet obt.	not yet obtained
13.11.2000	v	13:20	4.0	missdat	20	30	25	none	SSE	0	0
14.11.2000	v	10:10	0.6	0.6	35	40	37.5	none	E	100	0
15.11.2000	no data-collection due to wind detention										
16.11.2000	v	09:10	0.9	1.5	0	3	1.5	none	SSE	10	0
17.11.2000	v	12:40	2.5	2.4	0	2	1	increasing	NNE	100	LS
18.11.2000	no data-collection due to wind detention										
19.11.2000	b	12:50	-1.0	-0.9	0	0	0	'gusty'	SW	100	0
20.11.2000	v	09:10	-1.2	-1.2	10	10	10	none	NW	100	S
21.11.2000	v	12:50	2.5	3.3	0	5	2.5	none	SSE	100	LS
22.11.2000	no data-collection due to snowstorm										
23.11.2000	b	09:31	-1.0	-2.4	8	10	9	none	WNW	100	0
24.11.2000	v	08:27	0.0	-0.2	5	10	7.5	none	NW	25	0
25.11.2000	b	14:17	4.7	6.3	0	0	0	none	none	100	0
26.11.2000	v	14:15	6.3	9.5	0	0	0	none	none	25	0
27.11.2000	v	08:24	2.0	0.5	10	15	12.5	none	SW	25	0
28.11.2000	b	08:35	0.9	0.4	20	25	22.5	none	SW	100	0
29.11.2000	v	15:15	0.4	-0.6	0	0	0	none	none	100	LS
30.11.2000	no data-collection for logistic reasons										
01.12.2000	v	09:59	3.0	3.4	15	20	17.5	none	NE	100	0
02.12.2000	b	09:50	0.7	0.2	0	5	2.5	none	NW	100	0
03.12.2000	no data-collection for logistic reasons										
04.12.2000	v	14:30	3.2	2.1	0	5	2.5	none	NE	100	R/ Dr

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[25] With respect to climatic conditions upon departure (from tent and thus colony), some data loss was due to signs of an abrupt change in the weather, usually snowstorms.

Table 4-5: Weather Data Collected – 2000. (page 2 of 2)

Departure date	visit/ baseline	time dep	temp (°C) ground dep	temp (°C) 0.5m dep	wind-speed (km/ h) min dep	wind-speed (km/ h) max. dep	mean wind-speed (km/ h) dep	wind-gusts (km/ h) dep	wind-direction dep	cloud-cover (%) dep	precipitation dep; 0=none LS=light snow S=snow R=rain; Dr=drizzle
12.11.2000	b	18:32	1.7	not yet obt.	10	20	15	30	not yet obt.	not yet obt.	not yet obtained
13.11.2000	v				16:17				data of entire record missing		
14.11.2000	v	12:38	0.7	0.4	40	50	45	none	missdat	100	Dr
15.11.2000	no data-collection due to wind detention										
16.11.2000	v	12:10	1.7	6.9	0	5	2.5	10	SSE	20	0
17.11.2000	v	15:18							possibility of imminent snowstorm prevented collection of weather data		
18.11.2000	no data-collection due to wind detention										
19.11.2000	b	15:40	-0.9	-1.0	30	40	35	none	SW	100	0
20.11.2000	v	12:01	-0.2	2.4	0	0	0	none	none	75	0
21.11.2000	v	15:10	4.2	4.0	1	1	1	none	SSE	100	LS
22.11.2000	no data-collection due to snowstorm										
23.11.2000	b	12:29	0.0	0.1	0	0	0	none	missdat	missdat	LS
24.11.2000	v	10:55	3.9	4.1	0	5	2.5	none	NW	50	0
25.11.2000	b	17:10	4.8	5.0	0	5	2.5	none	SW	50	0
26.11.2000	v	16:35	5.7	6.1	5	10	7.5	none	SW	50	0
27.11.2000	v	11:00	6.4	5.2	5	10	7.5	15	SW	50	0
28.11.2000	b	11:15	2.0	0.6	25	30	27.5	35	SW	75	LS
29.11.2000	v	17:55	1.5	0.4	0	0	0	none	none	75	0
30.11.2000	no data-collection for logistic reasons										
01.12.2000	v	12:25	3.4	1.6	10	15	12.5	20	NE	100	0
02.12.2000	b	12:25	1.6	-0.3	10	15	12.5	none	NW	100	0
03.12.2000	no data-collection for logistic reasons										
04.12.2000	v	16:45	2.0	0.6	10	10	10	none	NE	100	R

Table 4-6: Weather Data Collected – 2001. arr: arrival, dep: departure; temp: temperature; min.: minimum, max.: maximum, mean: mean from min.&max.; gusts: abrupt increases in wind speed; missdat: data missing. (page 1 of 2)

Arrival date	visit/ baseline	time arr	temp (°C) ground _arr	temp (°C) 0.5m arr	wind-speed (km/ h) min. arr	wind-speed (km/ h) max. arr	mean wind-speed (km/ h) arr	wind-gusts (km/ h) arr	wind-direction arr	cloud-cover (%) arr	precipitation arr 0=none LS=light snow S=snow R=rain; Dr=drizzle
22.11.2001	b	10:54	6.5	0.8	30	30	30	40	WSW	75	0
23.11.2001	v	15:00	1.9	2.6	35	40	37.5	none	W	75	0
24.11.2001	v + b	08:43	2.8	2.1	0	0	0	15-20	NW	75	0
25.11.2001	b	09:35	1.5	1.1	15	15	15	15-20	WNW	100	0
25.11.2001	b	14:30	4.7	4.2	0	0	0	none	WNW	100	Dr
26.11.2001	v + b	08:46	1.3	1.3	10	12	11	15	WSW	75	0
27.11.2001	no data-collection due to wind detention (ca. 90 km/ h)										
28.11.2001	b	14:51	0.5	0.3	40	45	42.5	$\geq$ 50	W	100	Dr
29.11.2001	no data-collection due to wind detention										
30.11.2001	no data-collection for logistic reasons										
01.12.2001	v + b	11:50	3.2	3.0	33	40	36.5	$\geq$ 45	WNW	25	0
02.12.2001	v + b	12:50	3.7	2.3	30	35	32.5	40	W	100	0

Table 4-6: Weather Data Collected – 2001. (page 2 of 2)

Departure date	visit/ baseline	time dep	temp (°C) ground dep	temp (°C) 0.5m dep	wind-speed (km/ h) min. arr	wind-speed (km/ h) max arr	mean wind-speed (km/ h) dep	wind-gusts (km/ h) dep	wind-direction dep	cloud-cover (%) dep	precipitation dep 0=none LS=light snow S=snow R=rain; Dr=drizzle
22.11.2001	b	15:55	-0.1	-0.7	30	34	32	45	WSW	100	LS
23.11.2001	v	17:55	2.4	1.8	27	27	27	35-45	W	75	0
24.11.2001	v + b	12:55	4.2	5.5	5	5	5	12	W	0	0
25.11.2001	b	12:15	2.6	2.9	5	7	6	none	WNW	100	0
25.11.2001	b	16:50	4.1	3.4	3	3	3	none	WSW	100	LS
26.11.2001	v + b	12:55	0.4	1.5	0	0	0	none	none	100	S
27.11.2001	no data-collection due to wind detention (ca. 90 km/ h)										
28.11.2001	b	17:25	0	-0.1	30	35	32.5	50	W	100	0
29.11.2001	no data-collection due to wind detention										
30.11.2001	no data-collection for logistic reasons										
01.12.2001	v + b	15:40	2.6	1.9	30	40	35	50 and more	W(NW?)	100	0
02.12.2001	v + b	16:56	4.2	3.6	15	20	17.5	none	W	100	0

4.3 Data Transcription

4.3.1 Overview of Media and Methods Used For Data Transcriptions

A summary of **recording media** employed for collection of data and general information on methods used in data transcriptions is found in table 4-7.

N.b.: In the following sections, detailed information on **primary transcription** of data is provided, while descriptions pertaining to secondary transcriptions have been kept general at this stage.

Table 4-7: Recording Media and Methods Used For Data Transcriptions. ECG: electrocardiogram, display of heart rate.

Parameter	Recording Medium	Original Format of Data	Primary Transcriptions	Secondary Transcriptions
Penguin Behaviour s.l. (= behaviour s.s. and posture)	video	tape recordings	transcription matrices (paper)	Excel spreadsheets; SPSS spreadsheets
Penguin Heart Rate	artificial egg & data logger	voltage-files in Excel	ECG-graphs in Excel (beats per 20s)	Excel spreadsheets; SPSS spreadsheets
Conspecific Disturbance	video	tape recordings	transcription matrices (paper)	Excel spreadsheets; SPSS spreadsheets
Human Disturbance	field notebook	written notes, aligned with video/ logger		Excel spreadsheets; SPSS spreadsheets
Predators; Aircraft	video; field notebook	tape recordings; written notes	remarks column of transcription matrices (paper)	remarks column of spreadsheets

Secondary transcriptions to a large extent determine the structure of results to be presented, reflecting decisions made by the researcher in terms of definitions and final categories employed.

For this reason, mode and methods of secondary transcriptions should be well in the readers' minds during presentation of results. To facilitate this, details on secondary transcriptions have been placed into **methodological preludes** situated immediately before the respective results chapters. At the end of this chapter, schematic overviews of steps involved in data processing are presented separately for

1. focal groups (tab. 4-23),
2. focal-animal evaluations of behaviour elements, posture, and heart rate (tab. 4-21), and
3. focal-animal evaluations of behavioural, postural, and heart rate topography (tab. 4-22).

4.3.2 Behaviour/ Posture Data

> "To breed successfully, an Adélie Penguin must accomplish three major social tasks: secure and maintain a territory upon which to build a nest, develop a pair bond with an individual of the opposite sex so that eggs are laid in that nest, and with its mate coordinate the care of eggs and chicks. All of these tasks are accomplished by the exchange of information between the Adélie and its neighbors [sic], mate, and offspring." (AINLEY & al. 1983, ch. 5, p. 76)

For primary transcription of behaviour data, the video tapes were displayed on a **monitor** (Philips Type No. CM11342 / 00G; screen diagonal: 32 cm). This way, it was possible for a single observer to focus in turn on each individual in a group with equal accuracy.

4.3.2.1 Preliminary Categorisation of Behaviour/ Posture

After preliminary observations on Gentoo penguins[26] (*Pygoscelis papua*) at the Zoological Garden of Frankfurt/ Main (Germany) in 1999, a **preliminary categorisation** of behaviours was effected and subsequently 'fine-tuned on' Adélie penguins (*P. adeliae*) during the trial field season in another penguin colony on King George Island (1999/ 2000).

For THIS STUDY, Adélie penguin behaviour was categorised on the basis of the behaviours described in chapter 3. While categorisation of posture invariably comprised the categories prone (lying) and up (sitting or standing), behaviour categories differed according to transcription method (see respective sections).

Detailed **descriptions** of the behaviours/ behaviour elements have been provided in chapter 3. **Operationalised definitions** which permitted instant recognition of behaviour on a still screen during instantaneous scan sampling of focal groups are presented in box 4-2 (section 4.3.2.3). The rather extensive catalogue of **transcription rules** ('how to write down what') for behaviour elements and postures used with respect to focal animals is found in appendix 4-1.

4.3.2.2 General Considerations on Out-of-sight Time and Missing Data

> "Focal animals in the field [...] often disappear from view of the observer. Therefore, it is necessary to record the time intervals in each sample period that the individual being observed is out of sight; the result is 'missing data' for those time intervals. The sampling protocol/ data problem created by an animal under observation temporarily disappearing from view [...] has not been successfully resolved. That is, there is no truly valid procedure for determining what behaviour(s) occurred while that animal was out-of-sight. However,

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[26] Gentoos share the study penguins' genus and a number, though by no means all, of their behaviour traits (the Zoological Garden of Frankfurt/ Main does not keep Adélie penguins).

> there is a general relationship between the predictability of what behaviour occurred, the duration of behaviours most commonly observed, and the time the animal is out of sight."
> (LEHNER 1998, p. 193)

With respect to THIS STUDY, missing data could be attributed to two main causes. The first was **abiotic** and concerned the recording equipment. Wind speed during recordings ranged from 0 km/ h to above 50 km/ h, and due to the observer's role as 'visitor' in the majority of the recorded sessions, sudden gusts could lead to a 'temporary change of focus' of the video camera. Owing to low temperatures (around 0°C, and at times seriously exacerbated by wind chill), video and/or computer batteries would sometimes die off unexpectedly. Loss of data in these cases resulted in visits not always occurring at mid-recording as had initially been planned.

The second cause was **biotic/ 'penguinotic'**: Although the penguins investigated were incubating and thus necessarily intimately attached to their respective nests, they did not always humour the investigator by revealing that part of their anatomy most likely to inform her on their current behaviour, i.e. the head. Birds were considered **'out-of-sight'** when their position or posture made it impossible to accurately observe head movements. This happened for instance, when a bird turned the back towards the observer and simultaneously lowered the head. Penguins were similarly difficult to observe when their head and/or most of their body was hidden by neighbours or by non-breeders (conspecifics) standing or moving in front of them.

These episodes were noted and subsequently treated as **'missing data'** (for details see section 4.3.2.3.7, and section 4.3.2.4.10).

4.3.2.3 Focal Groups: Categorisation and Transcription of Behaviour/ Posture

Focal-Group evaluations aimed at detecting easily observable and clearly identifiable behaviours that permitted to gauge responses of penguin groups to human visitation. Behaviours meeting these requirements would be suitable for inclusion into codes of conduct for 'non-penguinologists', i.e., people not versed in the study of penguin behaviour.

Given the larger numbers of birds observed, only a limited number of indicators were chosen. While some of them had been suggested by the literature (i.e. headshakes, birds getting up), others had sprung to mind during direct observations (reconnaissance field season).

4.3.2.3.1 Datasets Transcribed

Only behaviour recordings that included a human visit were transcribed. Therefore, data were available for groups B and C (2000), and X and Y (2001), but not for group A which had been treated as the control group in 2000[27] and had not received any visits at all.

A total of 30 sessions (à 30 min; 2000: 20; 2001: 10) were included in focal-group evaluations. Table 4-8 gives a comprehensive overview on sessions transcribed per group.

Concerning groups **X** and **Y**, the **visiting regime** had remained the **same** throughout the (considerably shorter) fieldwork period. In contrast to that, groups B and C had been subjected to a **switch in visiting regime** from 27.11.2000 onwards, and for these two groups, reactions to

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[27] Preliminary evaluations between field seasons had confirmed that the variability in the incubating penguins' heart rate and behaviour and the variability in presence/ absence of 'visiting conspecifics' was so extensive that it was necessary for individual penguins to use the period immediately prior to a given visit as the 'control' with which to compare the behaviour and/or heart rate recorded during visits. The idea of a spatially separate control group was entirely abandoned in 2001.

different visiting regimes were also investigated. To distinguish within-group changes in visiting regime, the subsets are presented as **B_1**, **C_1** (when referring to the time **prior** to the switch in visiting regime) and **B_2**, **C_2** (when the time **after** the switch in visiting regime is concerned), respectively.

Table 4-8: Numbers of Behaviour Sessions Including a Human Visitation Event Transcribed per Focal Group. B, C, X, Y: study groups of penguins subjected to visitaiton; disc.: records were obtained but discarded prior to transcription.

Behaviour recordings in focal-group sampling; transcribed and analysed																			
Date / Group	13. Nov. 00	14. Nov. 00	16. Nov. 00	17. Nov. 00	20. Nov. 00	21. Nov. 00	24. Nov. 00	26. Nov. 00	27. Nov. 00	01. Dec. 00	04. Dec. 00	sum recordings per group	Date / Group	23. Nov. 01	24. Nov. 01	26. Nov. 01	01. Dec. 01	02. Dec. 01	sum recordings per group
B	1	1	1	1	1	1	1	1	1	1	1	11	X	1	1	1	1	1	5
C	1	disc.	disc.	1	1	1	1	1	1	1	1	9	Y	1	1	1	1	1	5
total behaviour recordings with human visitation transcribed and analysed: 30 (2000: 20; 2001: 10)																			

4.3.2.3.2 Identification Sketch, Assignment of Rows and Selection of Nests

Apart from the individuals chosen for Focal-Animal Sampling (see chapter 5.2, 5.3), none of the birds were artificially marked, and due to the lack of abundant natural markings in Adélie penguins, it was impossible to quantify the 'intersessional' number of changes in the incubating individuals observed (unless a nest relief occurred within the recorded observation session). Nor was it possible to collect individual information over time.

In contrast to that, the pattern of nesting territories was more easily discernible. Therefore, the birds were grouped by **rows** according to increasing distance from colony edge and therefore source of disturbance. The first four rows were included in the investigation. At the beginning of transcriptions, a **sketch** of the recorded section of the colony (fig. 4-7) served to assign rows of increasing distance to the source of human disturbance. Row 1 (R1) represented the nests on the edge of the colony; row 2 (R2) comprised those nests separated from direct approach of the human visitor(s) by one nest in front of them, and so on until row 4 (R4).

For each recorded session, **nests** clearly displayed on the video screen (i.e., not obscured by other nests) were chosen in each row (minimum: 3; maximum: 16, medians: R1=4, R2=6, R3=6, R4=7), extending from the edge of the colony inwards up to the fourth row of nests. These nests were marked on the monitor[28] and subsequently the respective birds' behaviour was noted for every session.

The total number of birds transcribed (rows 1-4) ranged from 11 to 48 (median: 23) for Instantaneous-Scan Sampling (ISS, six behaviour states and two postures) and from 10 to 46 (median: 22) for All-Occurrences Sampling (AOS, 'occurrence of headshakes', behaviour event). Although a minimum of three nests per row was selected at the beginning of the transcription of each recorded session, the behaviour of some birds was at times **impossible to transcribe** (see section 4.3.2.3.7). Even though the camera angle captured progressively more birds in the rows further inside the colony, in these rows progressively more birds also turned out to be 'temporarily inevaluable[29]' so that the **effective median** number of nests (i.e. the median number of incubating penguins whose behaviour could be categorised in each row at a given sampling point) was the

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[28] using non-permanent markers in different colours

[29] e.g., head hidden by incubating birds from other nests after changing position

same for all rows (median R1=R2=R3=R4: 4) with respect to **ISS**. Due to the distinctiveness of headshakes the **effective median** for **AOS** did not differ from the recorded median presented above.

Figure 4-7: Example of Sketches Used for Assignment of Rows. Sketches were drawn at the beginning of each data transcription and permitted inter-sessional comparison of row and nest assignments. This sketch depicts one session at group Y. The grey arrow indicates direction from which visitors approached. C: conspecifics currently not engaged in incubation; rows were differently coloured for better discrimination, and nest codes in the sketch reflect colours used (r: red = R1, o: orange = R2, y: yellow = R3, b: blue = R4).

4.3.2.3.3 Primary Transcription Procedure

Focal-group primary data transcriptions were performed on 30 min sessions of taped behaviour for all four groups alike[30].

For **Focal-Group All-Occurrences Sampling** (AOS, primary transcriptions; occurrence of headshakes), the sampling intervals lasted 30 s. Within each **interval**, data were transcribed chronologically and individually (e.g., headshake performed by individual on nest r1, followed by individual on nest b5, followed by individual on nest o4, etc.; see above, fig. 4-7).

Each sampling interval concluded with the scan sampling point, i.e. **Instantaneous-Scan Samples** (ISS, ‘six plus two’ categories, s.b.) were taken at the half and full minute. At each sampling **point**, data were transcribed as sums per row (e.g., R1-’alert’: 2, R1-’rest&Co’: 1, etc., see exemplary matrix in appendix 4-2).

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[30] … even though longer sessions had been recorded for groups X and Y.

4.3.2.3.4 Categorisation, Operationalisation, and Primary Transcription of Behaviour Aspects

During focal-group transcriptions, **three aspects** of ‘behaviour s.l.’ (p.106, footnote 12; q.v.) were distinguished, viz., behaviour **states**, behaviour **events** and **postures**. The aspect ‘states’ held six categories of mutually exclusive behaviours which (with the exception of ‘flippers up’) represented different behaviour systems. With respect to the aspect ‘events’, only one behaviour element was sampled, viz., occurrence of headshakes (tab. 4-9). The aspect ‘posture’ specified whether a given bird was ‘prone’ (lying) or ‘up’ (sitting or standing).

Definitions used to identify behaviours are provided in box 4-2.

Table 4-9: Categorisation of Adélie Penguin Behaviour Used in Focal-Group Transcriptions.

Aspect	Category	Behaviour Observed
Behaviour state	alert	vigilance (large or small head turns, scans)
	agonistic	gape, point, alternate-stare, sideways-stare, bill-to-axilla
	flippers up	flippers held up or moving up and down
	preen	preening (manipulation of plumage)
	manipulate	nest, egg or chick manipulation
	rest & Co	resting, sleeping, yawning, 'non-committal' movements
Behaviour event	headshakes	head-, head-shoulder- or full-body-shakes
Posture	prone	lying
	up	sitting, standing

4.3.2.3.5 Operational Definition of Behaviours

To meet the requirements of Instantaneous-Scan Sampling, behaviours had to be defined in such a way that recognition on the still screen was possible. Operational definitions are given in box 4-2.

4.3.2.3.6 Behaviour Aspects – Outlook on Secondary Transcription

Instantaneous-Scan Sampling data (behaviour states; postures) were matricised (spreadsheets, Microsoft, 1997/ 2003, see exemplary matrix in appendix 5.1-1; SPSS 10-14) the way they had been originally transcribed (i.e. numbers of incubating penguins per row assigned to each category). All-Occurrences Sampling data (occurrence of headshakes) were entered as **One-Zero Sampling** data.

Proportionalisations (Penguin-Unit-Index, q.v. in Methodological Prelude, chapter 5.1.1) were calculated prior to analyses.

Details on secondary transcriptions are provided in the **methodological prelude** at the beginning of chapter 5.1.1. A schematic overview of steps involved in data processing (transcriptions, analyses, and visualisation) is found at the end of this chapter (tab. 4-23).

4.3.2.3.7 Out-of-sight Time and Missing Data

Wind-induced **camera** vibrations rendered categorisation of some behaviour states problematic or impossible. At other times, **birds** turned their backs to the camera or were obscured by non-incubating conspecifics or other breeding birds. (t.b.c.)

Box 4-2: Operational Definitions of Behaviours Used in Focal-Group Transcriptions. Definitions for behaviour states were operationalised to fit the requirements of Instantaneous-Scan Sampling; i.e., to be recognised on the still screen.

Behavioural states:

‘**alert**’: The bird’s head was level with their body or raised, turning or turned towards the source of the disturbance. The eyes were open, the bill closed, and the flippers down. The bird was either prone or up, focusing on something/ someone outside their nest.

‘**agonistic**’: The bird was ‘frozen’ in any of the movements associated with agonistic behaviour (bill-to-axilla, sideways or alternate stares, point or gape; see detailed descriptions in chapter 3.1.4). The bird was either prone or up, focusing on something/ someone outside their nest.

‘**flippers up**’[31] : The bird was up (sitting or standing) with their flippers raised/ caught waving about, focusing on something/ someone outside their nest.

‘**preen**’: The bird’s head was directed towards their own body, with the bill touching or close to the feathers. This behaviour occurred predominantly, but not exclusively, when the bird was up.

‘**manipulate**’: The bird’s head was down, with the neck pulled in or elongated and the bill touching or close to a nest[32] or their eggs. The bird was either prone or up, focusing on something inside or close to their nest (i.e. potential new nest stones in the vicinity or the neighbouring nests).

‘**rest&Co**’: A bird assigned to this category was either ‘resting’/ ‘sleeping’, or it showed one of various small and/or rather short-lasting comfort behaviours (e.g. ‘yawn’, ‘snap[33]’, ‘stretch’, see detailed descriptions in chapter 3.1.4). For this, the bird was either prone or up. Broadly speaking, the category ‘rest&Co’ reflected a state of ‘non-committedness’ i.e., the bird was not observably directing their attention to any source/ stimulus in particular.

Behavioural event:

‘**headshakes**’: The head was moved briefly and rapidly from side to side, thus appearing as a blurred image on screen; the movement/ blur would at times include the shoulders (head-shoulder shake) or the whole body (ruffle-shake).

Postures:

‘**prone**’: The bird was lying on their nest.

‘**up**’: The bird was sitting or standing on their nest.

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[31] This category was chosen, because in the reconnaisance field season, birds during disturbance had frequently been observed to engage in slow- or rapid-wing-flaps (which otherwise may occur in various behaviour systems, such as pair formation and pair bond maintenance or comfort).

[32] not necessarily their own…

[33] briefly opening and closing the bill

Concerning Instantaneous-Scan Sampling (behaviour states, sampling points at each half and full minute), a bird's behaviour could only be assigned to any of the categories if their head was seen 'unfuzzily'. For each sampling point, the number of breeding birds per row whose behaviour was impossible to evaluate was therefore subtracted from the total number of breeding birds per row. Proportions were calculated from the number of breeding birds visible (Penguin-Unit-Index, q.v.; Methodological Prelude in chapter 5.1).

Instantaneous-Scan Samples were **discarded** whenever the video image was illegible (blurred due to wind effects/ camera movement/ heavy snowfall) or battery exchange had to take place at that time.

In contrast to that, the occurrence of headshakes (behaviour event, AOS intervals from full to half-minute and from half to full minute) usually remained distinct even on wind-affected tape-sections, and headshakes were visible even if the bird was turning their back. All-Occurrences Sampling

Table 4-10: Overview of Period Durations and Missing Data for 30 Sessions of Focal-Group Sampling. pre-visit: time prior to visitation; post-visit: time after end of visit; missing data within recording: intranscribable periods within the total time; pt: sampling point(s); int: sampling interval(s). Instantaneous-Scan Sampling points occurred every 30 s (at :30 and :00); All-Occurrences Sampling intervals lasted 30 s; B_1/ C_1, B_2/ C_2: In groups B and C, the visiting regimes had been switched after two-thirds of the observation period.

date of recording	focal group	duration (min) per period				missing data within recording (pt; int)
		pre-visit	during-visit	post-visit	total	
13.11.2000	B_1	00:11:30	00:11:30	00:07:00	00:30:00	pre: 1 int, dur: 1+2+2+1 int
13.11.2000	C_1	00:07:00	00:11:00	00:07:00	00:25:00	dur: 0 pt/ 1+1 int
14.11.2000	B_1	00:08:00	00:11:00	00:11:00	00:30:00	pre: 1 pt/ 2 int
16.11.2000	B_1	00:05:00	00:08:00	00:17:00	00:30:00	none
17.11.2000	B_1	00:14:00	00:07:30	00:08:30	00:30:00	pre: 2 pt/ 3 int
17.11.2000	C_1	00:06:30	00:09:00	00:11:00	00:26:30	pre: 0 pt/ 1 int
20.11.2000	B_1	00:12:00	00:07:30	00:10:30	00:30:00	pre: 1 pt/ 1 + 2 int
20.11.2000	C_1	00:10:30	00:09:30	00:10:00	00:30:00	pre: 1 pt/ 2 int
21.11.2000	B_1	00:11:00	00:08:00	00:11:00	00:30:00	pre: 1 pt/ 2 int
21.11.2000	C_1	00:11:00	00:10:00	00:09:00	00:30:00	pre: 7 pt/ 8 int
24.11.2000	B_1	00:04:30	00:07:30	00:14:00	00:26:00	none
24.11.2000	C_1	00:11:30	00:09:00	00:09:30	00:30:00	pre: 2 pt/ 3 int
26.11.2000	B_1	00:08:00	00:07:30	00:14:30	00:30:00	pre: 1 pt/ 1 + 2 int
26.11.2000	C_1	00:09:30	00:09:30	00:11:00	00:30:00	pre & post: 1 pt/ 2 int resp.
27.11.2000	B_2	00:02:00	00:08:00	00:12:30	00:22:30	none
27.11.2000	C_2	00:09:30	00:08:30	00:12:00	00:30:00	pre: 1 pt/ 1 + 2 int
01.12.2000	B_2	00:11:30	00:09:00	00:09:30	00:30:00	none
01.12.2000	C_2	00:08:30	00:08:30	00:13:00	00:30:00	none
04.12.2000	B_2	00:09:30	00:09:30	00:11:00	00:30:00	none
04.12.2000	C_2	00:13:30	00:08:30	00:08:00	00:30:00	pre: 1 + 3 pt/ 1 + 4 int
23.11.2001	X	00:10:00	00:09:30	00:10:30	00:30:00	pre: 1 pt/ 1 + 2 int
23.11.2001	Y	00:10:30	00:09:30	00:10:00	00:30:00	none
24.11.2001	X	00:10:00	00:09:30	00:10:30	00:30:00	none
24.11.2001	Y	00:10:00	00:10:00	00:10:00	00:30:00	none
26.11.2001	X	00:09:30	00:09:30	00:11:00	00:30:00	none
26.11.2001	Y	00:10:00	00:09:00	00:11:00	00:30:00	post: 7 pt/ 9 int
01.12.2001	X	00:04:30	00:08:30	00:17:00	00:30:00	post: 1 pt/ 0 int
01.12.2001	Y	00:10:00	00:09:00	00:11:00	00:30:00	pre: 3 pt/ 4 int
02.12.2001	X	00:10:00	00:09:00	00:11:00	00:30:00	post: 0 pt/ 1 int
02.12.2001	Y	00:10:30	00:08:30	00:11:00	00:30:00	none

intervals were rigorously **discarded** as soon as one or more seconds were missing. Generally, this led to more data loss in the All-Occurrences samples. Occasionally, however, the occurrence of headshakes could be accurately determined, while the exact categorisation of each bird's behaviour at the Instantaneous-Scan Sampling point was impossible.

Table 4-10 provides detailed information per session. **Descriptive statistics** concerning recording times and missing data (sampling intervals/ sampling points) are summarised in table 4-11.

Table 4-11: Statistical Details on Recording Times and Missing Data for 30 Sessions of Focal-Group Instantaneous-Scan Sampling and Focal-Group All-Occurrences Sampling. pre-visit: time prior to visitation; post-visit: time after end of visit; missing data: intranscribable periods within a 30 min session; pt: sampling point(s); int: sampling interval(s); min.: minimum; Q1/ Q3: first/ third quartile; med.: median; max.: maximum; n: number of sessions transcribed. Figures concerning visiting times are given in minutes.

	pre-visit	**during-visit**	**post-visit**	**total time**	**missing pt**	**missing int**
min.	00:02:00	00:07:30	00:07:00	00:22:30	0	0
Q1	00:08:07	00:08:30	00:10:00	00:30:00	0	0
med.	**00:10:00**	**00:09:00**	**00:11:00**	**00:30:00**	**1**	**3**
Q3	00:10:52	00:09:30	00:11:00	00:30:00	3	5
max.	00:14:00	00:11:30	00:17:00	00:30:00	15	15
n	30	30	30	30	30	30

4.3.2.4 Focal Animals: Categorisation and Transcription of Behaviour/ Posture

Focal-animal evaluations served to examine the intra-individual extent of consistency (across sessions) as well as the range of differences between individual penguins (synchronous recordings) subjected to similar sources of potential disturbance (i.e., human visitation, conspecifics, and predators/ aircraft). A third aim was to compare for each bird their reactions towards humans with those displayed towards conspecifics in both content (qualitative: comprising changes in intensity within[34] as well as between[35] comportment parameters) and magnitude (quantitative: measured values).

With the exception of two nests that had received an artificial egg in mid-study (viz., nests B33 and C11[36]), the bird resident on the nest during placement of the artificial egg had been paint-marked (see section 4.1.2.1.2). It was thus possible to collect **individual information** over time.

To maximise the chance of detecting individual differences, a relatively large number of potential indicators were subsequently analysed. As with focal-group evaluations, some of these indicators had been suggested by previous studies (e.g. headshakes, birds getting up; e.g., Ainley 1974, 1978; Jouventin 1982; Penney 1968; Sladen 1958), while others had sprung to mind during direct observations in the course of the reconnaissance field season.

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[34] e.g., more vigilance head turns in quicker succession; for agonistic behaviours from low to high: Bill-to-Axilla (BTA), Sideways Stare (SST), Alternate Stare (AST), Point (P), Gape (G)

[35] e.g., from resting to vigilance to agonistic behaviours

[36] for whom only the distinction between 'prior-to' and 'after' egg-insertion could reliably be made until next observed change-over

4.3.2.4.1 Datasets Transcribed

With respect to focal animals, transcriptions included behaviour recordings of entirely **undisturbed** birds (mainly group A[37]), recordings of birds **disturbed** 'only' **by conspecifics** and/ or **predators**, and recordings in which a **human visit** occurred (generally on top of conspecific disturbance). The first two are referred to as 'baseline' sessions. Recordings including a visitation event could be separated into three distinct periods, viz., pre-, during-, and post-visitation, with the first period completely comparable to 'baseline' scenarios, while the third period lacked the direct influence of the human disturbance stimulus, but was potentially influenced by its after-effects.

Table 4-12: Numbers of Behaviour Sessions Transcribed per Focal Animal. FA: focal animal; A, B, C, X, Y: study groups of penguins; 2000, 2001: year of data collection; [group-nest]-3: unidentified incubator; no: no fieldwork possible; dc: discarded for various reasons; 0: only heart rate-records were transcribable; vis: human visitation occurred; unvis: no human visitation occurred; numbers in brackets: single sessions. (page 1 of 2)

Behaviour sessions transcribed and analysed per FA; with (purple) and without (turquoise) human visitation																								
Day and Month **FA (Year)**	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	**sum sessions transcribed per FA**
A5-1 (2000) unvis				no	0	1	no	1	1	1	no	1	1	1	1	1			no			no		**9**
A5-2 (2000) unvis				no			no				no						1	1	no	1	dc	no	dc	**3**
A5-3 (2000) unvis	dc	dc	dc	no			no				no								no			no		**0**
A6-1 (2000) unvis		dc		no			no	1	1	dc	no	1	dc						no	1	dc	no	dc	**4**
A6-2 (2000) unvis			1	no	1	0	no				no			1	0				no			no		**3**
A6-3 (2000) unvis	dc			no			no				no					dc	dc	dc	no			no		**0**
B3-1 (2000) vis		1		no			no				no		1		1				no			no		**3**
B3-1 (2000) unvis	dc			no			no				no			1					no			no		**1**
B3-2 (2000) vis			1	no	1	1	no		1	1	no								no			no		**5**
B3-2 (2000) unvis				no			no	1			no	0							no			no		**1**
B3-3 (2000) vis				no			no				no					dc		dc	no	dc		no	dc	**0**
B3-3 (2000) unvis				no			no				no						dc		no		dc	no		**0**
B4-1 (2000) vis		dc	dc	no	1	dc	no		1	1	no								no			no		**3**
B4-1 (2000) unvis	dc			no			no	1			no								no			no		**1**
B4-2 (2000) vis				no			no				no		1		1	dc		dc	no	dc		no	dc	**2**
B4-2 (2000) unvis				no			no				no	1		dc			1		no		dc	no		**2**
B33-1 (2000) vis				no			no				no							dc	no	dc		no	dc	**0**
B33-1 (2000) unvis				no			no				no						dc		no		dc	no		**0**
B33-2 (2000) vis		1	1	no	1	1	no		dc	dc	no		1		1	dc			no			no		**6**
B33-2 (2000) unvis	dc			no			no	1			no	1		dc					no			no		**2**
C1-1 (2000) vis		1	dc	no	dc	0	no		1	dc	no		1		1				no			no		**4**
C1-1 (2000) unvis	dc			no			no	dc			no	1		dc					no			no		**1**
C1-3 (2000) vis				no			no				no					1		dc	no	dc		no	dc	**(1)**
C1-3 (2000) unvis				no			no				no						dc		no		dc	no		**0**
C2-1 (2000) vis		dc	dc	no	dc		no				no							dc	no	dc		no	dc	**0**
C2-1 (2000) unvis	dc			no			no				no						1		no		dc	no		**(1)**
C2-2 (2000) vis				no		1	no		1	1	no		1		1	1			no			no		**6**
C2-2 (2000) unvis				no			no	0			no	1		1					no			no		**2**
C11-1 (2000) vis				no			no				no				1	1		dc	no	1		no	dc	**3**
C11-1 (2000) unvis				no			no				no						dc		no		dc	no		**0**
C11-2 (2000) vis		dc	dc	no	dc	1	no		1	dc	no		1						no			no		**3**
C11-2 (2000) unvis	dc			no			no	1			no	1		dc					no			no		**2**

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[37] Located uphill, group A received considerably less conspecific attention than the other groups.

Table 4-12: Numbers of Behaviour Sessions Transcribed per Focal Animal. (page 2 of 2)

Behaviour sessions transcribed and analysed per FA; with (purple) and without (turquoise) human visitation																								
Day and Month **FA (Year)**	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	**sum sessions transcribed per FA**
X1-1 (2001) vis	2001: delayed arrival in the field											1	1		1	no		no	no			end of field-work		**3**
X1-1 (2001) unvis											2		1	2	dc	no		no	no					**5**
X2-1 (2001) vis												1	1		1	no		no	no					**3**
X2-1 (2001) unvis											2		1	2	0	no		no	no					**5**
X2-2 (2001) vis																no		no	no	1	1			**2**
X2-2 (2001) unvis																no	dc	no	no	1	2			**3**
X3-1 (2001) vis												1	1			no		no	no					**2**
X3-1 (2001) unvis											2		1			no		no	no					**3**
X3-2 (2001) vis															1	no		no	no	1	1			**3**
X3-2 (2001) unvis														2	dc	no	dc	no	no	1	dc			**3**
Y4-1 (2001) vis												1	dc		0	no		no	no					**1**
Y4-1 (2001) unvis											1		1	1	1	no		no	no					**4**
Y5-1 (2001) vis												1	1		1	no		no	no					**3**
Y5-1 (2001) unvis											1		1	2	1	no		no	no					**5**
Y5-2 (2001) vis																no		no	no	1	dc			**1**
Y5-2 (2001) unvis																no	0	no	no	1				**1**
Y6-1 (2001) vis												1	dc			no		no	no					**1**
Y6-1 (2001) unvis											dc		1	1		no		no	no					**2**
Y6-2 (2001) vis															dc	no		no	no	1	dc			**1**
Y6-2 (2001) unvis															1	no	dc	no	no	1				**2**
total behaviour sessions transcribed and analysed: 119 (2000: 66; 2001: 53)																								
unvisited sessions: 64 (2000: 31; 2001: 33); visited sessions: 55 (2000: 35; 2001: 20)																								
total number of FAs (excl. unidentified and single-session birds: 23 (2000: 13; 2001: 10)																								

N.b.: The **switch in visiting regime** mentioned for focal groups B and C could not be analysed with respect to focal animals, as the majority of these sessions had to be discarded, due to insufficient[38] visibility of focal birds.

Excluding unidentified focal animals and single sessions of identified focal animals, a total of 119 sessions were transcribed for focal-animal analyses (tab. 4-12). In 2000 (30 min-sessions), 35 sessions during which human visitation had taken place were complemented by 31 'baseline' sessions. The respective figures for 2001 (45 min-sessions) amounted to 20 visitation and 33 'baseline' sessions. Table 4-12 gives a comprehensive overview on sessions transcribed per focal animal.

4.3.2.4.2 Identification Sketch and Assignment of Nest Zones

At the beginning of transcriptions, a sketch manually copied from a screenshot of the recorded section of the colony (fig. 4-8) served to document the location of the current focal animal's nest within the colony, and their own initial orientation with respect to the camera. If possible[39], the sketch included at least three circles of 'surrounding' nests. On the sketch, these circles were marked and used to define concentric **'nest zones'** for determination of conspecific distance to the focal-animal nest (see section 4.3.4.2.2 for details). In accordance with the policy of minimum-

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[38] when focusing on only one bird, and evaluating behaviour on a second-by-second basis

[39] Natural boundaries (boulders, the colony edge) would at times prevent the inclusion of three nests.

impact, the nests of focal animals were exclusively situated in the first or second rows[40]. In the front, nest zones thus extended beyond the colony edge.

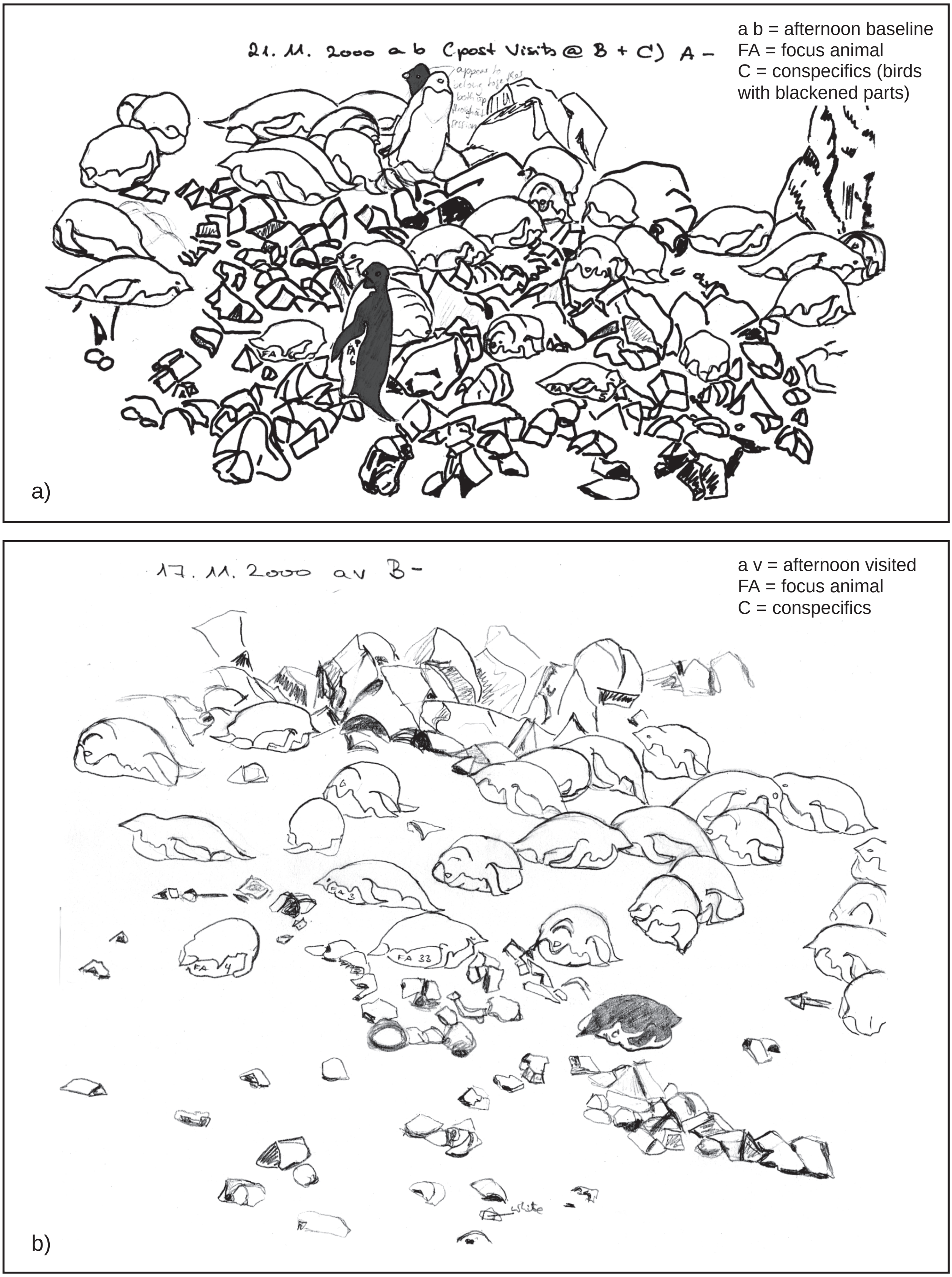

Figure 4-8 a-b: Examples of Identification Sketches Used for Transcription of Focal-Animal Behaviour/ Posture, and Conspecific Disturbance in Three Nest Zones.

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[40] These could be approached from the edge so that placement of artificial eggs did not require entering the colony.

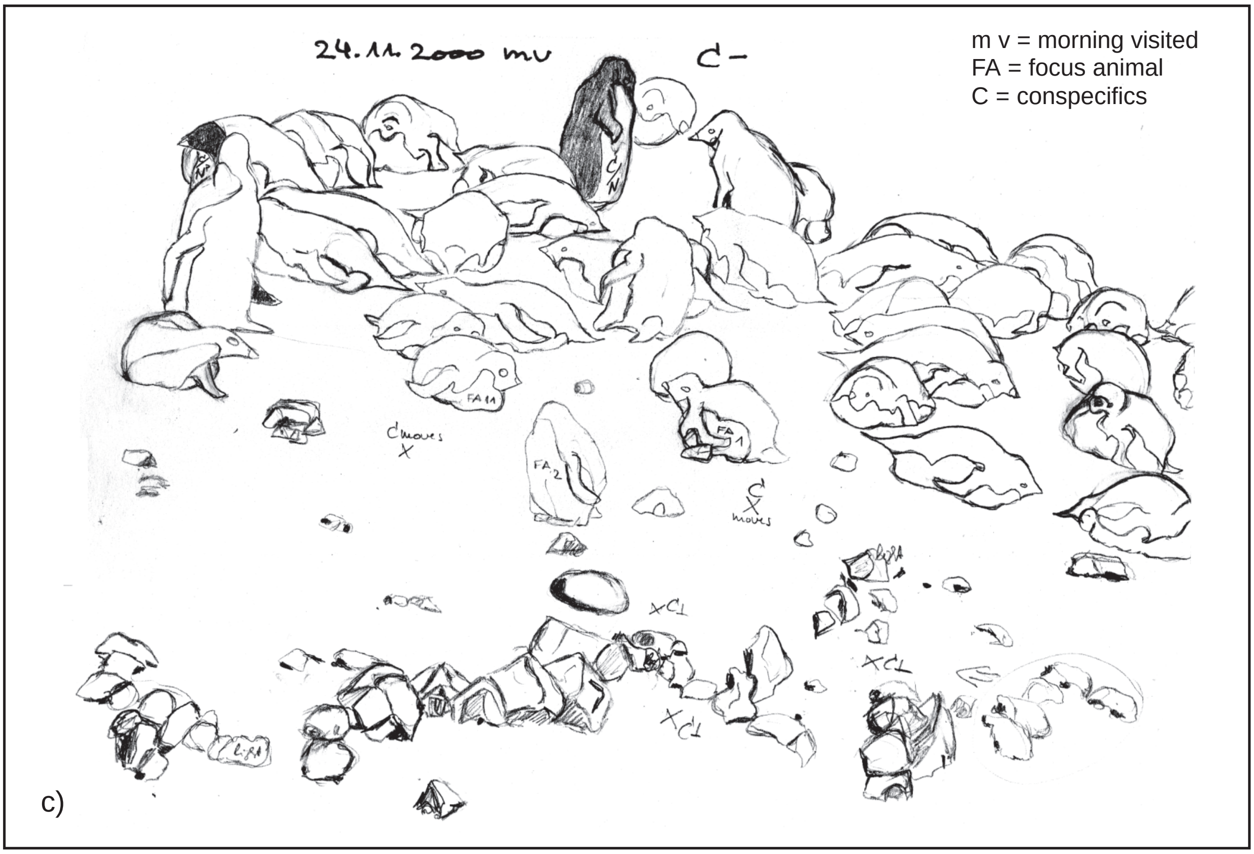

Figure 4-8 c: Examples of Identification Sketches Used for Transcription of Focal-Animal Behaviour/ Posture, and Conspecific Disturbance in Three Nest Zones.

4.3.2.4.3 Primary Transcription Procedure

Focal-animal data transcriptions were performed on 30 min (groups A, B and C) or 45 min (groups X and Y) periods of taped recordings.

During **primary transcriptions** (video data into hard-copy matrices), the focal animal's **orientation** relative to the video camera, their **posture** and the behaviour **element** currently being performed were written down second-by-second. The rules of assignment are listed in appendix 4-1. If a behaviour element continued for longer than a second, its onset and end were marked by dots to document its duration (fig. 4-9). Primary transcriptions thus yielded an unabridged and continuous behaviour record of the focal animal within the given time frame (i.e., 1,800 s and 2,700 s, resp.).

4.3.2.4.4 Categorisation and Primary Transcription of Behaviour/ Posture

For focal-animal **primary transcriptions** (i.e., classifying the FA's behaviour second-by-second), the transcriber needed to be able to identify and name each element of the behaviour displayed by an animal under observation.

Therefore, **behaviour elements** were noted according to ethograms[41] found in the literature (e.g., AINLEY 1974; JOUVENTIN 1982). Descriptions of the behaviour elements observed in THIS STUDY have been listed in chapter 3, and 31 categories are summarily presented in table 4-13. As to gradations in **intensity** (e.g., for egg/ nest manipulation: intentional vs. fully expressed; for vigilance: moderate vs. intense), and distinctions as regards **direction** (e.g., for head movements: level vs. rising/ descending; including neck extensions or not), these are described in detail in the transcription

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[41] Ethogram: Inventory, listing and describing all the behaviour patterns shown by a species (SLATER 1999).

rules provided in appendix 4-1. While a number of behaviour elements are in themselves ‘impossible to misunderstand’ (e.g., point, gape → agonistics), certain elements (e.g., head turns) may arise from different motivations (e.g., surveying the surroundings → alertness, i.e., vigilance; placing a nest stone → nest manipulation, i.e., breeding). A sequence of elements, however, usually gives a clear indication as to the contextual frame and underlying motivation.

Table 4-13: Categorisation of Adélie Penguin Behaviour and Posture as Used in Focal-Animal Primary Transcriptions. Head turns were only classified as vigilance behaviour if they did not occur in the performance of behaviours from other systems (e.g., breeding behaviour). Assignment of swallows depended on context (rest or comfort). Posture was noted in addition to behaviour elements. 1, 3: level head turns; 2, 4: head turns in conjunction with a raising of the head. K, KS, KK: coded by German terminology, i.e. Kopf-, Kopf-Schulter-, Kopf-Körper-Schütteln (headshake, head-shoulder-shake, head-body-shake = ruffle-shake); LD = Lone = ecstatic display.

Behaviour system/ Posture	Behaviour element/ Posture	Entry code
Rest/ Inactivity	no movements	[no entry]
	sleep	'asleep'
	small, non-committal movement	Sm
	swallow (depending on context, also in Comfort)	sl
	snap	'snap'
	bill tremor	BT
	bill shake	BS
Vigilance	large head turn (> 90°) not pertaining to other system	3 or 4
	small head turn (45°-90°) not pertaining to other system	1 or 2
	scan (< 45°)	Sc
Agonistics	gape	G
	point	P
	alternate stare	AST
	sideways stare	SST
	bill-to-axilla	BTA
Breeding	egg/ chick manipulation (may contain head turns)	Em
	shuffle	sh
	scratch	scr
	nest manipulation (may contain head turns)	Nm
	wing-flap (included in display)	WF
	loud and quiet mutual display	MD
	ecstatic display	LD
Comfort	preen	Pr
	headshake	K
	head-shoulder-shake	KS
	full-body-shake	KK
	forward-flipper-stretch	FFS
	backward-flipper-stretch	BFS
	(rapid-) wing-flap	(R)WF
	swallow (depending on context, also in Rest)	sl
	yawn	Y
Posture	prone	L
	up	S/ St

Behaviour systems[42, 43] were also noted during focal-animal primary transcriptions. These later served to group successive elements pertaining to the same behaviour system into phases. The resulting succession of phases is referred to as **behavioural topography** in THIS THESIS.

Posture was transcribed as either 'prone' (lying) or 'up' (sitting/ standing), with changes in relative position (with respect to the video camera) marked upon occurrence (see exemplary transcription sheet in appendix 4-4; fig. 4-9).

Figure 4-9 depicts 30 s of focal-animal behaviour and posture as entered into the primary transcription matrices.

01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
L	↗														S	↑					↖	L							
							Nm										Em												
3	●	●	●	●			1	●	2	●	1	2	1	●	●	4	1	●	1	1	●	1 & sh	1 & sh	1 & sh	1 & sh	2 & sh	● & sh		

↖↑: postural orientation relative to VC; ●: continuation of element

Figure 4-9: Example of 30 s of <u>Primary</u> Transcription of Focal-Animal Behaviour, Posture, and Relative Orientation. Time (in seconds) is displayed in the first row, the second row codes for posture and orientation, the third row depicts behaviour states if necessary for assignment of elements, which are entered into the fourth row. Entirely empty cells code resting behaviour/ no movement. Arrows denote postural orientation relative to video camera. 01-30: seconds of a given minute; L: prone, S: up; Nm: nest manipulation, Em: egg manipulation, sh: shuffle (rocking on egg), 1, 2, 3, 4: head turns of different extension and direction (unsuperscribed, these denote vigilance).

During **secondary transcriptions** (hard-copy matrices into Excel/ SPSS spreadsheets), the primary information was **summarised in different ways** depending on complexity (i.e., elements/ behaviour systems; s.b. for outline/ outlook). Matrices were created in Excel (1997, 2003) and/or SPSS (versions 10.0-14.0).

4.3.2.4.5 Behaviour Elements and Posture – Outline of Secondary Transcription

N.b.: Unlike for the other results chapters, an **outline** of (rather than merely an outlook upon) secondary transcriptions is given with respect to **behaviour elements/ posture** for the following reasons. Findings on some behaviour elements have appeared elsewhere (SCHUSTER 2008). Consequently, results concerning behaviour elements do not form part of the 'thesis proper'. Instead, a summary is provided in chapter 5.3.2, and the complete paper is found in appendix 5.2-1. Owing to limitations of space, however, the paper does not offer detailed information on data processing up to the stage of (self-explanatory) statistical analyses (i.e., correlations). For greater transparency, information on secondary transcriptions is provided here, and a **schematic overview** of steps involved in data processing (transcriptions, analyses, and visualisation) is presented at the end of this chapter (tab. 4-21).

For analyses of **behaviour elements**, secondary transcriptions were performed on 30 min (2000) and 45 min (2001) stretches of focal-animal data, respectively. The continuous flow of behaviour was 'broken down' into consecutive 20 s-intervals, and rates[44] (events) and durations (states;

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[42] In comparative ethology, behaviour systems constitute comprehensive behaviour categories which subsume behaviours based on the same or similar motivation(s) (MEYER 1984).

[43] behaviour systems = motivational systems = functional systems; originally named "Funktionskreise" by J. v. UEXKÜLL, 1921 (quoted in TEMBROCK 1982)

[44] rate: number of occurrences per unit of time; here: number of occurrences per 20 s-interval

grouped events, e.g., duration spent performing agonistic behaviours, the time spent performing large and small head turns during vigilance) of selected behaviour elements (table 4-14) were calculated per interval. **Posture** and number of posture changes (from ‘prone’ to ‘up’ and vice versa) per interval were also entered into the matrix.

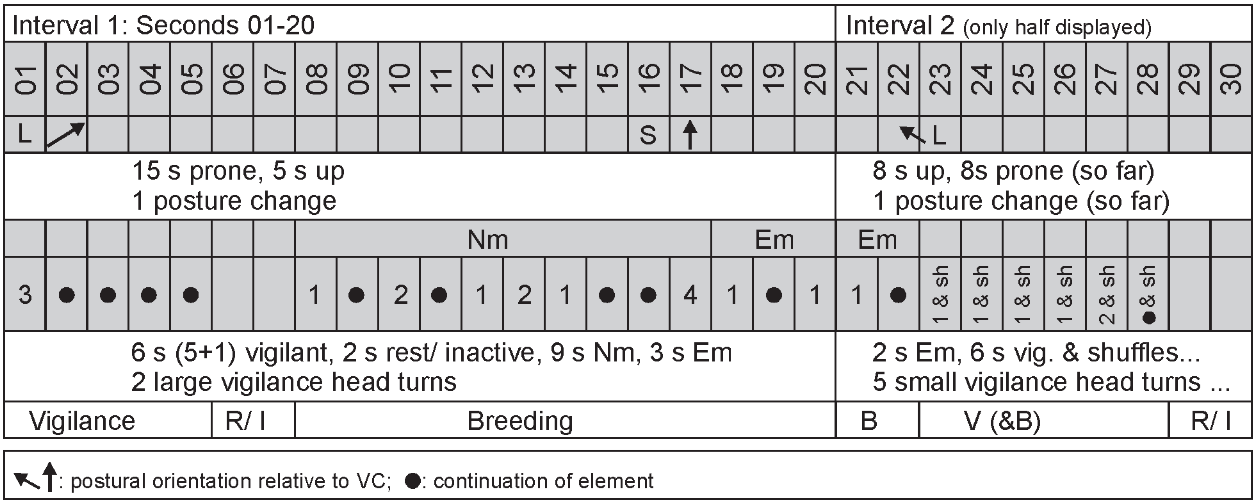
The procedure is illustrated in figure 4-10.

N.b.: Rather than being noted by frequency of single occurrences, the behaviour element **‘scan’** was matricised in terms of the number, duration and intensity of **scanning-phases**. An exhaustive definition of scanning-phases is given in appendix 4-1.

Figure 4-10 redisplays entries of primary transcription (grey-shaded rows; see figure 4-9) to subsequently illustrate conversions effected for entry into secondary matrices (unshaded rows). An exemplary matrix sheet is found in appendix 4-3.

Table 4-14: Focal-Animal Secondary Transcription – Behaviour Elements/ Posture. Rate and/or duration of selected behaviour elements were calculated for 20 s-intervals. The behaviour element ‘scan’ was evaluated in terms of rate and duration of scanning-phases. x: entered into secondary transcription matrices as rate and/or duration.

Behaviour System	Behaviour Element	Rate (frequency per 20 s-interval)	Duration (time per 20 s-interval)
Rest/ Inactivity	no movement		x
	sleep		
	small, non-committal movement		
	swallow		
	snap		
	bill tremor		
	bill shake		
Vigilance	large head turn	x	x
	small head turn	x	
	scan	scanning-phases	scanning-phases
Agonistics	gape	x	x
	point	x	
	alternate stare		
	sideways stare		
	bill-to-axilla		
Breeding	egg/ chick manipulation		x
	shuffle		x
	scratch		x
	nest manipulation		x
	wing-flap	x	x
	mutual display		x
	loud display		x
Comfort	preen		x
	headshake	x	x
	head-shoulder-shake	x	x
	full-body-shake	x	x
	forward-/ backward-flipper-stretch	x	x
	(rapid-) wing-flap	x	x
	swallow	not evaluated in context of Comfort (q.v. Rest)	
	yawn	x	x
Posture	prone/ up	rate of changes	x



<table>
<tr><td colspan="20">Interval 1: Seconds 01-20</td><td colspan="10">Interval 2 (only half displayed)</td></tr>
<tr><td>01</td><td>02</td><td>03</td><td>04</td><td>05</td><td>06</td><td>07</td><td>08</td><td>09</td><td>10</td><td>11</td><td>12</td><td>13</td><td>14</td><td>15</td><td>16</td><td>17</td><td>18</td><td>19</td><td>20</td><td>21</td><td>22</td><td>23</td><td>24</td><td>25</td><td>26</td><td>27</td><td>28</td><td>29</td><td>30</td></tr>
<tr><td>L</td><td>↗</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>S</td><td>↑</td><td></td><td></td><td></td><td></td><td>↖</td><td>L</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td colspan="20">15 s prone, 5 s up
1 posture change</td><td colspan="10">8 s up, 8s prone (so far)
1 posture change (so far)</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td colspan="10">Nm</td><td colspan="3">Em</td><td colspan="2">Em</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>3</td><td>●</td><td>●</td><td>●</td><td>●</td><td></td><td></td><td>1</td><td>●</td><td>2</td><td>●</td><td>1</td><td>2</td><td>1</td><td>●</td><td>●</td><td>4</td><td>1</td><td>●</td><td>1</td><td>1</td><td>●</td><td>1 & sh</td><td>1 & sh</td><td>1 & sh</td><td>1 & sh</td><td>2 & sh</td><td>● & sh</td><td></td><td></td></tr>
<tr><td colspan="20">6 s (5+1) vigilant, 2 s rest/ inactive, 9 s Nm, 3 s Em
2 large vigilance head turns</td><td colspan="10">2 s Em, 6 s vig. & shuffles...
5 small vigilance head turns ...</td></tr>
<tr><td colspan="5">Vigilance</td><td colspan="2">R/ I</td><td colspan="13">Breeding</td><td colspan="2">B</td><td colspan="6">V (&B)</td><td colspan="2">R/ I</td></tr>
</table>

↖↑: postural orientation relative to VC; ●: continuation of element

Figure 4-10: Example of 30 s of Secondary Transcription of Focal-Animal Behaviour, Posture, and Relative Orientation. Grey-shaded rows repeat entries of primary transcription (q.v.), unshaded rows illustrate conversion of information during secondary transcription with respect to analyses of behaviour elements and posture. Grey-shaded rows: Time (in seconds) is displayed in the second row, the third row codes for posture and orientation, the fifth row depicts behaviour states if necessary for assignment of elements, which are shown in the sixth row. The continuous flow of behaviour was broken down into 20 s-intervals (first row), and rates/ durations were calculated (fourth, seventh & eighth rows). Arrows denote orientation relative to video camera. 01-30: seconds of a given minute; L: prone, S: up; Nm: nest manipulation, Em: egg manipulation, sh: shuffle (rocking on egg), 1, 2, 3, 4: head turns of different extension and direction (unsuperscribed, these denote vigilance). R/ I: rest/ inactive, B: breeding, V: vigilance.

4.3.2.4.6 Behavioural and Postural Topography – Outlook on Secondary Transcription

As stated above, methods of transcription used for each level should be well in the readers' minds when results are presented. Descriptions here are kept to a minimum, and details are provided in **methodological preludes** placed at the beginning of each of the results (sub-)chapters. A **schematic overview** of steps involved in data processing (transcriptions, analyses, and visualisation) is found at the end of this chapter (tab. 4-22).

For analyses of behavioural/ postural **topography**, **secondary transcriptions** were performed on 30 min stretches of focal-animal data ('sessions'). With respect to data collected in 2001 (45 min per session), the behaviour and heart rate (q.v.) record available in primary transcriptions was 'trimmed' at the beginning and end so that, generally, the period of human visitation was situated approximately in the middle of the remaining record.

Secondary transcriptions focused on duration and distribution of each of the **behaviour systems** as well as both **postures**. The 'flow' of behaviour systems and postures before, during and after disturbance was assessed to examine changes in overall performance.

As mentioned in chapter 2, in this context, **'flow'** combines the overall presence and prevalence ('amount'/ extent) of behaviours belonging to a given behaviour system with the duration of phases found within that system as well as capturing changes between different behaviour systems (e.g., comfort 2 min, vigilance 20 s, comfort 10 s, vigilance 5 s) and 'smoothness' of transitions between systems (e.g., instant switches between systems, interruptions of one system by elements pertaining to another system, transitionary phases comprising elements of two different systems).

Taken together, these are referred to as the animal's **behavioural topography**, and visualised as follows: Behaviour systems are coded numerically, with numbers attempting to reflect differences in focus and intensity (from 'none or noncommittal' during resting to 'outward towards a likely threatening stimulus' during offensive agonistics). If plotted against time, each behaviour system is thus represented by a straight line on a system-specific horizon, while changes are indicated by the line 'jumping' from one horizon to the next.

Behavioural and postural **topography** (for heart rate, q.v.) were **examined on three levels**, viz., 1. qualitatively[45] in terms of changes in intensity, and quantitatively in terms of number of birds displaying these changes (visual appraisal; key question: How many do respond?), 2. quantitatively on the level of occurrence/ prevalence of behaviour systems (comparison of magnitudes of changes in behaviour systems and posture; key question: How much do they respond?), and 3. quantitatively on the level of phases (distribution of phase/ state durations; key question: In what way do they respond?).

Each of these questions was addressed by looking at all focal birds together, and by examining differences between regimes. The chapter concludes with a comprehensive comparison of reactions to the different visiting regimes detected on the different levels.

■ Qualitative Overview: Visual Appraisal of Changes in Behaviour and Posture during Human Visitation and/ or Conspecific Presence

Visual Appraisal constituted a **qualitative, 'graphical' examination** of changes in behaviour, posture, and heart rate (q.v.) before, during, and after human visitation. Following this, the question of consistency of these changes across focal animals was addressed **quantitatively** (key question: How many?).

For visualisation, two Excel spreadsheets per session were created into which focal-animal parameters (1st spreadsheet) and disturbance parameters (2nd spreadsheet) were entered second-by-second. Focal-animal behaviour systems were assigned to topographical classes (tab. 5.3.1-2, chapter 5.3.1.1). These were complemented by focal-animal posture (prone or up; per second) and heart rate (20 s-counts, q.v.). The second Excel spreadsheet contained information on conspecific and human disturbance (tab. 5.3.1-3, chapter 5.3.1.1). In addition to that, the rare recordings of skua (*Catharacta* spp.) presence on the ground, skua low[46] overflights or aircraft noise were also noted in this spreadsheet.

Creation of Topography Charts: Each of the spreadsheets was split into three 10-minute sections so that the graphs created served to represent time before, during, and after human visitation.

Definitions: The definitions employed to assess behaviour and heart rate (q.v.) in visual appraisal are presented in box 5.3.1-1 (chapter 5.3.1.1).

Visiting Stage Performance Indicator Value (VS-PIV): The Visiting Stage Performance Indicator Value represented the stages of the visit unweighted by visitor number or conduct (tab. 5.3.1-3, chapter 5.3.1.1).

Conspecific Movement Measure (CMM): The Conspecific Movement Measure served to assess intensity and consistency of conspecific movement prior to human visitation for each session (tab. 5.3.1-4, chapter 5.3.1.1).

Visual Appraisal – Procedure: Each chart was scaled to fit an A3 sheet[47]. Using A3-printouts of the 51 sessions, 9 comportment[48] parameters, comprising 7 behavioural parameters, as well as

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[45] i.e., looking for increases/ decreases without calculating the magnitude of these changes

[46] Low overflights by Southern giant petrels (*Macronectes giganteus*) were not observed.

posture and heart rate were examined (tab. 5.3.1-5; chapter 5.3.1.1). To increase **intra-observer reliability** across sessions, visual appraisal of each of the 51 sessions was performed twice (1-51 first time, 1-51 second time), and the consensus was used for comparisons.

Before as well as after human visitation, visual appraisal was undertaken for five 2 min-intervals. During human visitation, focal-animal behaviour, posture and heart rate (q.v.) were examined separately for each stage of the visit. Occurrences of natural disturbance (and aircraft noise – extremely rarely encountered) were likewise examined in that manner.

Colour Codes: Two sets of colour codes were used to depict ‘pre-visit status’ (blue-green colour range) and changes found during and after visitation (yellow-red colour range; see tabs. 5.3.1-6 and 5.3.1-7 in chapter 5.3.1.1).

■ Quantitative Comparison of Prevalence of Behaviour Systems and Postures Exhibited before, during, and after Human Visitation

Comparison of prevalence of behaviour systems and one of the two postures[49] before, during, and after human visitation examined between-period changes in proportional occurrence of each parameter (key question: How much?).

This was complemented by analyses of heart rate variation (q.v.) using 8 (descriptive) statistical parameters.

Friedman-tests were performed to examine consistency of direction of between-period changes, while **boxplots** visualised the magnitude of period differences found for each parameter.

■ Distribution of Phase/ State Durations of Behaviour Systems and Postures before, during, and after Human Visitation

Distribution of phase/ state durations of behaviour phases, posture states and heart rate phases (q.v.) before, during, and after human visitation assessed **changes in ‘flow’**, by examining the duration and occurrence/ absence of phases and states for each period (key question: In what way?).

Behaviour:

For the purpose of THIS THESIS, the **definitions** pertaining to behaviour phases are presented in box 5.3.3-1(chapter 5.3.3.1).

Prior to determination of phase durations, the behaviour record was **‘condensed’** using a step-wise procedure (box 5.3.1-2 in chapter 5.3.3.1).

Period differences were examined after **overlaps** (i.e. phases across period boundaries) had been accommodated by assigning the entire phase to the period within which its greater proportion[50] had occurred.

Behaviour phase durations were assigned to three duration classes, each of which was divided into three subclasses (tab. 5.3.3-1; chapter 5.3.3.1).

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[47] An example is presented in chapter 5.3.1.1, fig. 5.3.1-2; all graphs are available in appendix 5.3.1-1.

[48] In THIS THESIS, the term ‘comportment’ is employed to summarily refer to behaviour, posture, and heart rate.

[49] which were mutually exclusive (i.e., the bird could be either prone or up)

Posture:

Posture state was **classified** as either ‘prone’ or ‘up’ (the latter combining sitting and standing postures). **Overlaps** regularly reached far into the following period(s). Rather than trying to assign them to any one period, these were included in analyses of change frequencies only, but did not feature in analyses of state durations.

Posture state durations were likewise assigned to three <u>duration classes</u>, each of which was divided into three <u>subclasses</u> (tab. 5.3.3-2; chapter 5.3.3.1). Due to their greater range, class borders differ from those chosen for behaviour phases.

4.3.2.4.7 Out-of-sight Time and Missing Data

The behaviour of a focal animal was at times impossible to transcribe, basically for the same reasons as stated with respect to focal-group transcriptions (camera vibrations, bird’s head down and back to observer, bird hidden by conspecifics). Periods of ‘intranscribability’ ranged from 1 s (e.g., a pass<u>ing</u> conspecific) to the entire recording session (e.g., a pass<u>ive</u> conspecific).

Out-of-sight time was noted in the hard-copy matrix. It was transcribed in accordance with the rules outlined in appendix 4-1.

With respect to **<u>behaviour elements</u>**, missing **single seconds** were ‘extrapolated[51] ’ if the behaviour before and after them was identical. Whenever the behaviour elements differed in intensity but belonged to the same behaviour system (e.g., alternate stare and sideways stare are both agonistic elements, with the former being more intense), the second in question was awarded to the less intense category. If behaviour systems before and after were different, however, the second was recorded as ‘unaccounted for’. Likewise, no attempts were undertaken to ‘guess’ the contents of **longer stretches of invisibility**. Periods of **intermittent visibility** (generally caused by moving conspecifics) were included if time accounted for exceeded 2 s, was at least as long as the time unaccounted for on one side and at the same time longer than that unaccounted for on the other (e.g., 4 s of invisibility, followed by 4 s of visibility, followed by 2 s of invisibility). Periods unaccounted for were summed up per interval, and the entire 20 s-interval was **discarded** if it contained less than 10 s of visible behaviour.

As for **<u>posture</u>**, missing data only occurred at the beginning or end of sessions so that no rules for extrapolation needed to be devised for evaluation in conjunction with behaviour elements or behavioural topography (q.v.).

Concerning **<u>behavioural topography</u>**, missing behaviour data were coded as 0 (zero) to allow for visual assessment of reliability of the remaining behaviour. Rules for extrapolation/ inclusion were identical to those outlined for behaviour elements.

In the <u>topography charts</u> (behaviour), any **missing seconds** have been left unchanged. Stretches of missing data are indicated by cross-hatched blocks.

N.b.: For tabulated <u>visual appraisal</u> of changes in the different behaviour systems and posture (and heart rate, q.v.), the term ‘n.a.’ (not applicable) was used to indicate either that the focal animal had not been seen in the respective interval or that the behaviour system focused on had not been observed throughout the session.

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[50] to adjust for different recording times per period

[51] read: ignored

For quantitative comparison of prevalence (behaviour), any **missing seconds** were left unchanged and thus did not enter calculations.

With respect to phase durations (behaviour), one and two **missing seconds** enclosed in phases or interruptions were treated like 'impurities' (box 5.5.5-1; chapter 5.3.3.1). No attempt was undertaken to assign longer stretches of missing data.

Phases bordering onto missing data were only included in counts for phase durations, if they exceeded 20 s. Rules employed to accommodate missing behaviour data during evaluations of phase durations are explained in box 4-3).

Box 4-3: Rules Employed to Accommodate Missing Behaviour Data During Evaluations of Phase Durations. A series of three identical capital letters denotes a phase (successive behaviour elements pertaining to the same behaviour system: AAA). A series of constantly changing elements pertaining to different behaviour systems codes for an interruption (DEF). M: missing data; A, B, C, D, E, F: different behaviour systems; (A)A: 1 s or 2 s of behaviour system A.

Missing Data
AAA **M(M)** AAA ➔ M → A (one long phase)
AAA **M(M)** CCC ➔ M → C (phase C is extended)
DEF **M(M)** DEF ➔ M → DEF (interruption is extended)

(A)A **M** A(A) ➔ M → A (one long phase)
(A)A **M** C(C) ➔ M → C (phase C is extended)
(D)E **M** F(E) ➔ M → DEF (interruption is extended)

(A)A **MM** A(A) ➔ A → M (missing data are extended on both sides)
(A)A **MM** C(C) ➔ A(A) and C(C) → M (missing data are extended on both sides)
(D)E **MM** F(E) ➔ (D)E and F(E) → M (missing data are extended on both sides)

N.b.: Phases bordering onto missing data were only included in counts for phase durations, if they exceeded 20 s.

4.3.3 Heart Rate Data

4.3.3.1 Transcription of Heart Rate

Focal-animal heart rate evaluations served to examine the intra-individual extent of consistency (across sessions) as well as the range of differences between individual penguins (synchronous recordings) with respect to their physiological reactions when subjected to similar sources of potential disturbance (i.e., human visitation, conspecifics, and predators/ aircraft). A third aim was to compare for each bird their heart rate reactions towards humans with those displayed towards conspecifics.

4.3.3.1.1 Datasets Transcribed

As described for transcriptions of behaviour responses (section 4.3.2.4), heart rate transcriptions included recordings of entirely **undisturbed** birds (mainly group A), recordings of birds **disturbed** ‘only’ **by conspecifics** and/ or **predators**, and recordings during which a **human visit** occurred (generally on top of conspecific disturbance). The first two are jointly referred to as ‘baseline’ sessions. Recordings including a visitation event could be separated into three distinct periods, viz., pre-, during-, and post-visitation, with the first period completely comparable to ‘baseline’ scenarios, while the third period lacked the direct influence of the human disturbance stimulus, but was potentially influenced by its after-effects.

Excluding unidentified focal animals and single records obtained from identified focal animals, heart rate records from a total of 88 sessions were transcribed for focal-animal analyses. In 2000 (30 min-sessions; 11 FA), records comprised 26 visitation and 31 ’baseline’ sessions. The respective figures for 2001 (45 min-sessions; 5 FA) amounted to 12 visitation and 19 ’baseline’ records. Table 4-15 gives a comprehensive overview of sessions transcribed per focal animal.

4.3.3.1.2 Assignment of Nests

In accordance with the policy of minimum-impact, the artificial eggs had been inserted into nests of the first or second rows[52] . As already mentioned, the birds resident on the nest during placement of the artificial egg had been paint-marked (with the exception of two nests, viz., nests B33 and C11[53]), and could thus be distinguished from their naïve partners. As preliminary analyses revealed substantial day-to-day variation between heart rate (and behaviour) of individuals, but no consistent differences between birds that had or had not been present during placement of the artificial egg, this distinction is not referred to in analyses.

4.3.3.1.3 Primary Transcription Procedure

Prior to transcription, the original heart rate files were resaved in .xls-format, and 20 s-graphs were created (amounting to 90 graphs for each 30 min session; 135 graphs for each 45 min session). As depicted in figure 4-11, heart rate signals varied in overall form, voltage and amplitude[54] . While it was possible for a human brain to extract the relevant information from different ‘types’ of heart rate signals, the computer programme designed for this purpose sadly failed to accomplish that feat. For transcriptions used in comparison with results from behaviour element evaluations, **20 s-**

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[52] These could be approached from the edge of the colony so that placement of artificial eggs did not require entering the colony.

[53] for whom only the distinction between ‘prior-to’ and ‘after’ egg-insertion could reliably be made until a change-over was observed

[54] To some extent this is caused by the position of the bird’s brood patch relative to the window of the artificial egg.

intervals of heart rate were thus **manually counted** (i.e. 5,130 graphs for 57 sessions à 30 min, and 4,185 graphs for 31 sessions à 45 min).

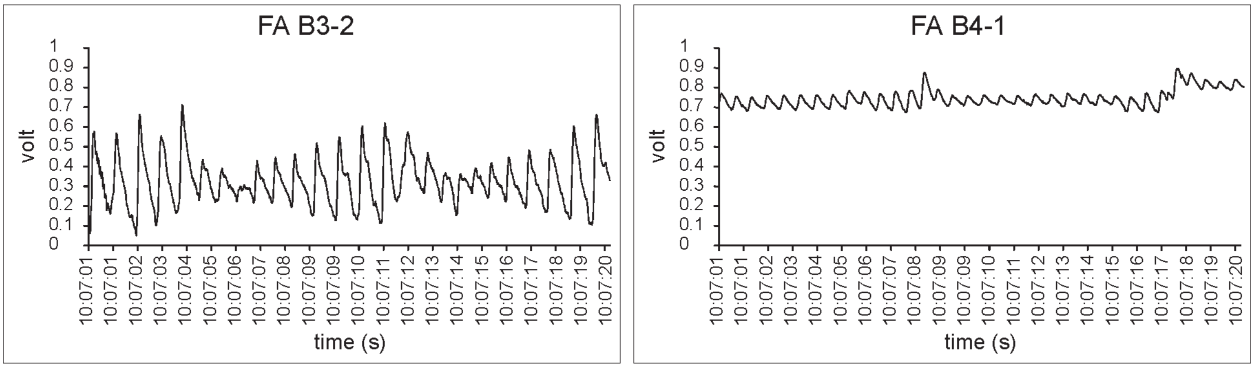

Figure 4-11: 'Real-Time' Heart Rate of Two Focal Animals (B3-2, B4-1). For each focal animal, 20 s of heart rate, representing the counting interval used, are depicted. As can be seen, the signals vary in overall form, amplitude, and absolute voltage. FA: focal animal.

Table 4-15: Numbers of Sessions Transcribed for Focal-Animal Heart Rate Records. FA: focal animal; A, B, C, X, Y: study groups of penguins; 2000, 2001: year of data collection, [group-nest]-3: unidentified incubator; no: no fieldwork possible; dc: discarded for various reasons; no egg: no artificial egg inside nest; vis: human visitation occurred; unvis: no human visitation occurred; numbers in brackets: sessions excluded from analyses. (page 1 of 2)

Heart rate recordings transcribed and analysed per FA; from sessions with (purple) and without (turquoise) human visitation

Day and Month / FA (Year)	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	sum recordings obtained per FA
A5-1 (2000) unvis				no	1	1	no	1	1	1	no	1	1	1	1	1			no			no		**10**
A5-2 (2000) unvis				no			no				no						1	1	no	1	dc	no	dc	**3**
A5-3 (2000) unvis	dc	dc	dc	no			no				no								no			no		**0**
A6-1 (2000) unvis		dc		no			no	dc	1	dc	no	1	dc						no	1	dc	no	dc	**3**
A6-2 (2000) unvis			1	no	1	1	no				no			1	1				no			no		**5**
A6-3 (2000) unvis	dc			no			no				no					dc	dc	dc	no			no		**0**
B3-1 (2000) vis		1		no			no				no		1		1				no			no		**3**
B3-1 (2000) unvis	dc			no			no				no			1					no			no		**1**
B3-2 (2000) vis			1	no	1	1	no		1	1	no								no			no		**5**
B3-2 (2000) unvis				no			no	1			no	1							no			no		**2**
B3-3 (2000) vis				no			no				no					dc		dc	no	dc		no	dc	**0**
B3-3 (2000) unvis				no			no				no						dc		no		dc	no		**0**
B4-1 (2000) vis		dc	dc	no	1	dc	no		1	1	no								no			no		**3**
B4-1 (2000) unvis	dc			no			no	1			no								no			no		**1**
B4-2 (2000) vis				no			no				no		1		1	dc		dc	no	dc		no	dc	**2**
B4-2 (2000) unvis				no			no				no	1		dc			1		no		dc	no		**2**
B33-1 (2000) vis				no			no				no							dc	no	dc		no	dc	**0**
B33-1 (2000) unvis				no			no				no						dc		no		dc	no		**0**
B33-2 (2000) vis				no			no				no								no			no		**no egg**
B33-2 (2000) unvis				no			no				no								no			no		**no egg**

Table 4-15: Numbers of Sessions Transcribed for Focal-Animal Heart Rate Records. (page 2 of 2)

Heart rate recordings transcribed and analysed per FA; from sessions with (purple) and without (turquoise) human visitation

Day and Month / FA (Year)	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	sum recor--dings ob-tained per FA
C1-1 (2000) vis		1	dc	no	dc	1	no		1	dc	no		1		🟪				no			no		**4**
C1-1 (2000) unvis	dc			no			no	dc			no	1		dc					no			no		**1**
C1-3 (2000) vis				no			no				no					🟪		🟪	no	🟪		no	🟪	**no egg**
C1-3 (2000) unvis				no			no				no								no			no		**no egg**
C2-1 (2000) vis		dc	dc	no	dc		no				no							dc	no	dc		no	dc	**0**
C2-1 (2000) unvis	dc			no			no				no						(1)		no		dc	no		**no analyses**
C2-2 (2000) vis				no		1	no		1	1	no		1		1	1			no			no		**6**
C2-2 (2000) unvis				no			no	1			no	1		1					no			no		**3**
C11-1 (2000) vis				no			no				no				1	1		dc	no	1		no	dc	**3**
C11-1 (2000) unvis				no			no				no						dc		no		dc	no		**0**
C11-2 (2000) vis		🟪	🟪	no	🟪	🟪	no		🟪	🟪	no		🟪						no			no		**no egg**
C11-2 (2000) unvis	🟦			no			no	🟦			no	🟦		🟦					no			no		**no egg**
X1-1 (2001) vis	2001: delayed arrival in the field											1	1		1	no		no	no			end of field-work		**3**
X1-1 (2001) unvis											1		1	2	dc	no		no	no					**4**
X2-1 (2001) vis												1	1		1	no		no	no					**3**
X2-1 (2001) unvis											2		1	2	1	no		no	no					**6**
X2-2 (2001) vis																no		no	no	1	1			**2**
X2-2 (2001) unvis																no	dc	no	no	1	2			**3**
X3-1 (2001) vis												dc	dc			no		no	no					**0**
X3-1 (2001) unvis											dc		dc			no		no	no					**0**
X3-2 (2001) vis															dc	no		no	no	(1)	dc			**no analyses**
X3-2 (2001) unvis														dc	dc	no	dc	no	no	dc	dc			**0**
Y4-1 (2001) vis												dc	dc		(1)	no		no	no					**no analyses**
Y4-1 (2001) unvis											dc		dc	(1)	(1)	no		no	no					**no analyses**
Y5-1 (2001) vis												1	1		1	no		no	no					**3**
Y5-1 (2001) unvis											1		1	2	1	no		no	no					**5**
Y5-2 (2001) vis																no		no	no	1	dc			**1**
Y5-2 (2001) unvis																no	1	no	no	dc				**1**
Y6-1 (2001) vis												dc	dc			no		no	no					**0**
Y6-1 (2001) unvis											dc		dc	(1)		no		no	no					**no analyses**
Y6-2 (2001) vis															dc	no		no	no	dc	dc			**0**
Y6-2 (01) uv															dc	no	dc	no	no	dc				**0**

sum of heart rate recordings transcribed and analysed: 88 (2000: 57; 2001: 31)

recordings during unvisited sessions: 50 (2000: 31; 2001: 19);
recordings during visited sessions: 31 (2000: 26; 2001: 12)

total number of FAs (excl. unid. and single- or zero-session birds: 16 (2000: 11; 2001: 5)

4.3.3.1.4 Heart Rate in Conjunction with Behaviour Elements – Outline of Secondary Transcriptions

Manually counted 20 s-values were extrapolated to beats-per-minute (bpm) and correlated with results on behaviour elements, posture, and disturbance which had likewise been evaluated for 20 s-intervals (tab. 4-21; summary in chapter 5.2.3; paper in 5.2-1).

4.3.3.1.5 Heart Rate Topography – Outlook on Secondary Transcriptions

In conjunction with behavioural topography (q.v.) evaluations which examined the 'flow' of behaviour, a different approach was needed to reflect accompanying heart rates. Rather than extrapolating to beats-per-minute values (bpm), heart rate **counts per 20s** were plotted 'as counted'. The reader is asked to keep in mind that for comparison with published studies the respective values need to be multiplied by three. Representation of focal-animal heart rate generally depicted 'real 20 s-counts' (heartbeats counted for 20 s), and, in some instances, 30 s-counts calculated to fit 20 s-requirements (see explanation in section 4.3.3.1.6).

- **Qualitative Overview: Visual Appraisal of Changes in Heart Rate during Human Visitation and/or Conspecific Presence**

For visual appraisal, pre-visit heart rate (comprising approximately 10 min per session) was **classified** as either 'undulating regularly', increasing or decreasing across five 2 min-intervals. During-visit as well as post-visit heart rate was then compared to pre-visit heart rate (increasing/ decreasing/ no change; see tab. 5.3.1-5, in Methodological Prelude, chapter 5.3.1.1).

- **Comparison of Variation in Heart Rate before, during, and after Human Visitation with Variation in 'Baseline' Heart Rate**

Apart from looking at between-period changes in heart rate (e.g., for mean or maximum values obtained), analysis of the magnitude of heart rate variation was extended to not only include **visited** sessions but also **'baseline'** sessions, i.e. sessions without human visitation. This way, it was possible to additionally compare heart rate variation across periods (before, during and after human visitation) with variation recorded for successive 10 min-intervals (without any human interference). Comparisons of heart rate variation were analysed using a total of **8 statistical parameters** (chapter 5.3.2.1).

- **Distribution of Phase Durations of Heart Rate before, during, and after Human Visitation**

Mean Resting Heart Rate (RHR) was determined (chapter 5.3.3.1), and **RHR ±2 SD** was taken as the 'tolerance band' for delineating three heart rate categories used for further analyses: below RHR ±2 SD, within RHR ±2 SD, and above RHR ±2 SD (NEEBE & HÜPPOP 1994; also see ELLENBERG & al. 2006, 2009).

Heart rate **phases** constituted lengths of time spent in a given category. **Phase durations** invariably lasted (multiples of) 20 s. In case of **overlaps**, i.e. phases across period boundaries, the entire phase was assigned to the period within which its greater proportion had occurred[55].

Heart rate phase durations were assigned to three duration classes, each of which was divided into three subclasses. Accommodating 20 s-intervals and a greater range (than behaviour phases), the classes presented in table 5.3.3-4 (chapter 5.3.3.1) resulted.

4.3.3.1.6 Missing Data

Three phenomena accounted for the greatest part of lost data: 1. Overwriting (technical/ computer-based error), 2. signal death (electronic systems failure), and 3. signal obfuscation (illegibility).

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[55] Proportions, rather than absolute time, were used to adjust for different recording times per period.

1. Several times, the last heart rate **file** recorded prior to a computer breakdown was **overwritten** by the first heart rate file after restart. These files were irretrievably lost.
2. **Signal death** occurred when an egg temporarily succumbed to the unfavourable climatic conditions; resurrection was at times possible by switching the egg-powering battery off and on again. This in itself resulted in a brief interruption of the signal, which, however, was preferable to longer-term loss of information. **Brief periods of inevitable data loss** (< 10 s) were also caused by manually saving one file and opening another. Both kinds of interruptions of the data stream were measured in the graph (length in mm). The same lengths were then measured before and after the loss, and the heartbeats of these were counted. The mean of the two values was taken to represent the number of heartbeats during signal loss (Prof. Dr. R.C. SCHROTER, pers. comm.).
3. **Signal obfuscation** was caused by the focal animal's moving on the nest, their getting up, or their brood patch not quite covering the window in the artificial egg[56]. Signal obfuscation was treated in the following ways:

   - The attempt to Fourier-transform **long periods of indistinct heart rate** to extract the underlying sinus-waves (programme MATLAB, release 5.3) did not render the resolution required to examine fluctuations in heart rate, and was consequently **abandoned**. These data were unavailable for analyses.
   - Signal obfuscation **for up to one second** was counted through, provided the general heart rate was well legible. If not, the disturbance was treated as described for brief periods of data loss.
   - **Short periods** of obfuscation (< 10 s; e.g., the focal animal briefly shifting on the egg) were likewise treated as described for brief periods of data loss.
   - If signal obfuscation occurred **in two consecutive 20 s-intervals** (i.e., in the beginning of the first and towards the end of the second interval) and these contained an unbroken heart rate record between them, this period was counted and the value given as an average for both intervals. In these cases, the available heart rate record had to at least contain 20 s; if records of, e.g., 30 s were available, the entire record would be counted and the resulting number of beats calculated to fit 20 s requirements. Stretches of **less than 15 s of continuous heart rate**, however, were considered invalid as a potential counting error was judged too severe[57]. These were consequently discarded.

With respect to **phase durations**, one or two missing 20 s-values (**M**) were counted through, if the following applied:

1. Heart rate before as well as afterwards could be assigned to the same category: →above-above-**M**-above-above, and <u>simultaneously</u>
2. phase duration before and afterwards was at least twice the duration of the missing value(s): → within (40s)-**M (20s)**-within (60s).

No attempt was undertaken to account for other types of missing data (longer stretches/ missing values between different phase categories). These were omitted from analyses.

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[56] N.b.: Infrared sensors do not take this kind of intrusion lightly.

[57] Recapitulation: One miscounted beat in 20 s will change the bpm-value by ±3 beats; one miscounted beat in 10 s will augment the counting error to ±6 beats.

4.3.4 Disturbance Data

4.3.4.1 Preliminary Categorisation of Disturbance: Identification of Components

> "Disturbance: 1. A change, or alteration, whether as the result of internal or external action, from a condition of order, repose, or peace to one of agitation or disorder. 2. The act of effecting this change." (Webster 2003)
>
> "Human disturbance is any human activity that changes the contemporaneous behavior [sic] or physiology of one or more individuals within a breeding colony of waterbirds." (Nisbet 2000)

During preliminary categorisation, four different **components of disturbance** were identified.

In this study, the term **type of disturbance** is used primarily to refer to the different ***'disturbing agents'*** relevant to this investigation, viz., humans and non-incubating penguins (mainly conspecifics, on a very few occasions congeners), and, to a lesser extent, predators and aircraft. Secondarily, with respect to humans, it serves to distinguish two pre-defined ***forms of conduct*** (silent and slow vs. loud and fast).

Next, the **number of 'disturbers'** (number of beings causing the disturbance) was considered relevant (humans, conspecifics).

Furthermore, **distance from the source** of disturbance, and the **duration of exposure** to disturbance were taken into account.

4.3.4.2 Final Categorisation and Operationalisation of Disturbance

The final categorisation of disturbance, its transcription as well as the calculation of total disturbance performance indicator values (operationalisation) differed for focal groups and focal animals due to the different sampling methods employed,

N.b.: In this thesis, the term 'operationalisation' is used for both a priori and a posteriori defined operators and thus includes human visitation (a priori) as well as conspecifics (a posteriori). For each operator, the term 'categorisation' is used to refer to distinct categories. Disturbance by predators/ aircraft did not receive any operationalisation, although for skuas, the qualitative distinction between overflights of different height and presence on the ground was made.

4.3.4.2.1 Human Disturbance

Disturbance types: In both years, the effects of ***two*** contrasting ***types of visitor conduct*** were recorded. Throughout visits of the type ***silent and slow***, movements and noise were kept to a minimum, movement towards (approach) and away from (retreat) the penguin group visited occurred at a slow pace; at the given distances, the visitor(s) stood or knelt quietly, avoiding 'sideways' movement (movement which did not change the distance to the colony edge).

In contrast to that, the conduct type ***loud and fast*** had the visitor(s) approach and retreat at a brisk pace. During the entire visit, they did not keep their voice(s) down, continued to move around at the given distances ('sideways' movement), and also occasionally abruptly extended their arms (waving, pointing).

Number of ‘disturbers’: Visiting experiments limited the number of human visitors to either ***one*** (‘1 person’) or ***three*** (‘3 persons’).

Visiting regimes: A total of ***four ‘visiting regimes’*** were examined. In 2000, the two different types of conduct described above were displayed by a single visitor, and the regimes were termed *‘**1 person, silent and slow**’* (1 P, S&S) and *‘**1 person, loud and fast**’* (1 P, L&F), respectively. The same types of human conduct were repeated in 2001, but this time the number of visitors was augmented to three (see fig. 4-5) resulting in the regimes *‘**3 persons, silent and slow**’* (3 P, S&S) and *‘**3 persons, loud and fast**’* (3 P, L&F).

Distance from the source of disturbance: Distance was measured between visitors and the edge of the colony. For visiting experiments, ***three distances*** had been predetermined, viz., ***15 m***, ***5 m***, and ***3 m*** (s.b.). Distances were ‘sign-posted’ by small piles of pebbles and rocks. Additionally, human visitors moved between these distances during ***approach*** and ***retreat***.

Duration of exposure to the disturbance: Visits followed a standard ***time-space protocol***.

The Human visitor(s) left the tent (through the back-’door’), walked round the tent, and approached group B (2000) or group X (2001) in a straight line. With respect to group C (2000) and group Y (2001), visitor(s) left the tent and walked along the foot of the hill opposite the study colony until they could approach the group in a straight line as well (see chapter 3.2.2.3, fig. 3-25).

At the three predetermined distances from the colony edge (15 m, 5 m, and 3 m, resp.), visitor(s) spent two minutes each. Retreat from the closest distance likewise occurred in a straight line but did not include any in-between stops. Time to the nearest second was noted separately for each of the distances, approach and retreat. Total time of visit depended on visitor speed as well as the distance between group and tent.

Duration of behaviour and heart rate recordings: To gauge the magnitude of the impact of human visitation (changes between pre- and during-visitation), the immediacy/ delay of waning of responses after stimulus withdrawal (changes between during- and post-visitation) and the speed of recovery (absence/ persistence of changes between pre- and post-visitation), penguin heart rate and behaviour were recorded for some time before[58] and after the visits (2000: 10 min before, 10 min after; 2001: 20 min before, 15 min after). To facilitate comparisons, analyses presented here were performed on 30 min of behaviour and heart rate regardless of duration of original transcriptions. Details on visiting schedule and visiting regimes are presented in table 4-16.

Recapitulation: In 2000, groups B and C were subjected to a **switch in visiting regime** after approximately two thirds of the fieldwork period, resulting in two datasets each for group B (B_1: ‘1 person, loud and fast’, B_2: ‘1 person, silent and slow’) and group C (C_1: ‘1 person, silent and slow’, C_2: ‘1 person, loud and fast’). The switch mainly affected **focal group** transcriptions, as post-switch recordings had to be discarded for most **focal-animal** transcriptions due to insufficient visibility of respective FAs. Because of logistical and climatic problems, fieldwork in 2001 (groups X and Y) started late in the Adélie penguins’ incubation period. Since the visiting schedule introduced during the previous season (visits once a day for two successive days, followed by ‘baseline’ recording) was to be adhered to for comparative purposes, it was impossible to repeat the switch (tab. 4-16).

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[58] The pre-visitation period also served to collect information on individual resting heart rate (Baldock & Sibly 1990) and ‘baseline’ behaviour and helped to accommodate susceptibility of heart rate to climatic conditions (Culik & al. 1989).

Table 4-16: Human Visitation Schedule and Visiting Regimes. Recordings with (purple) and without (turquoise) human visitation per group. A, B, C, X, Y: study groups of penguins; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime, unvis: no human visitation occurred; 2000, 2001: year of data collection; no: no fieldwork possible; dc: discarded for various reasons; L&F: loud and fast, S&S: silent and slow; 1 P: one visitor, 3 P: three visitors.

Human visitation schedule and visiting regimes: recordings with (purple) and without (turquoise) human visitation per group

Group (Year) \ Day and Month	12 Nov.	13 Nov.	14 Nov.	15 Nov.	16 Nov.	17 Nov.	18 Nov.	19 Nov.	20 Nov.	21 Nov.	22 Nov.	23 Nov.	24 Nov.	25 Nov.	26 Nov.	27 Nov.	28 Nov.	29 Nov.	30 Nov.	01 Dec.	02 Dec.	03 Dec.	04 Dec.	**total unvis**	**total vis**
A (2000) unvis	1	1	1	no	1	1	no	1	1	1	no	1	1	1	1	1	1	1	no	1	1	no	1	**18**	**0**
B_1 (2000) unvis/ 1P, L&F	1	1	1	no	1	1	no	1	1	1	no	1	1	1	1									**4**	**8**
B_2 (2000) unvis/ 1P, S&S																1	1	1	no	1	1	no	1	**2**	**4**
C_1 (2000) unvis/ 1P, S&S	1	1	1	no	1	1	no	1	1	1	no	1	1	1	1									**4**	**8**
C_2 (2000) unvis/ 1P, L&F																1	1	1	no	1	1	no	1	**2**	**4**
X (2001) 3P, S&S	2001: delayed arrival in the field											1	1		1	no		no	no	1	1	end of field-work			**5**
X (2001) unvis											2		1	2	1	no	0	no	no	1	2			**9**	
Y (2001) 3P, L&F												1	1		1	no		no	no	1	1				**5**
Y (2001) unvis											1		1	2	1	no	1	no	no	1				**7**	
total recordings with human visitation: 34 (2000: 12 L&F, 12 S&S; 2001: 5 L&F, 5 S&S)																									
total recordings without human visitation: 46 (2000: 30; 2001: 16)																									

4.3.4.2.2 Conspecific[59] Disturbance

Conspecifics were **defined** as being birds of the same species, currently not engaged in incubation. No distinction was made between non-breeders/ failed breeders and breeding birds not on the nest (i.e., the partner was incubating). The empirical approach to recording conspecific actions was dealt with differently during focal-group and focal-animal analyses.

Disturbance type: Although conspecifics also differed in ***conduct***, they could not be induced to collectively display these differences on cue. Conspecific conduct did not feature with respect to focal groups (i.e., conspecific presence only). As for focal animals, differences used to categorise conspecific conduct included ***speed*** of movement (stand/ lie, walk, run) and selected ***behaviours*** (e.g., stand up from previously prone position, fight, nest stone theft at the focal animal's nest).

Number of 'disturbers': Movements of conspecifics were not channelled or otherwise manipulated, and the number of conspecifics present **fluctuated** naturally. 'Boundaries' for inclusion of conspecifics into transcriptions were devised for focal groups and focal animals, respectively:

For focal groups, the first and last nest within each row constituted the limits on the left and right. To the front, some space was included in front of the first row; to the back, the fifth row of nests marked the exclusion line (fig. 4-12).

As for focal animals, all conspecifics present within the three concentric nest zones depicted in figure 4-13 were included.

Distance from the source of disturbance: The colony edge did not pose a limit to conspecifics, i.e., non-incubating conspecifics were found throughout the colony.

With respect to entire focal groups, distance measurements for individual conspecifics were therefore considered rather pointless: Examination of the behaviour of each of a number of conspecifics

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[59] The reader is kindly asked to keep in mind that during human visitation, conspecifics usually (per)formed the background disturbance on top of which the other type occurred.

towards each of a number of incubating birds and subsequent translation into a value representing the impact on the group as a whole was outside the scope of this investigation. Instead, the number of conspecifics present within focal-group 'boundaries' was noted separately for six areas (outside colony, colony edge-R1, R1-R2, R2-R3, R3-R4, R4-R5) delineated in accordance with the rows (fig. 4-12).

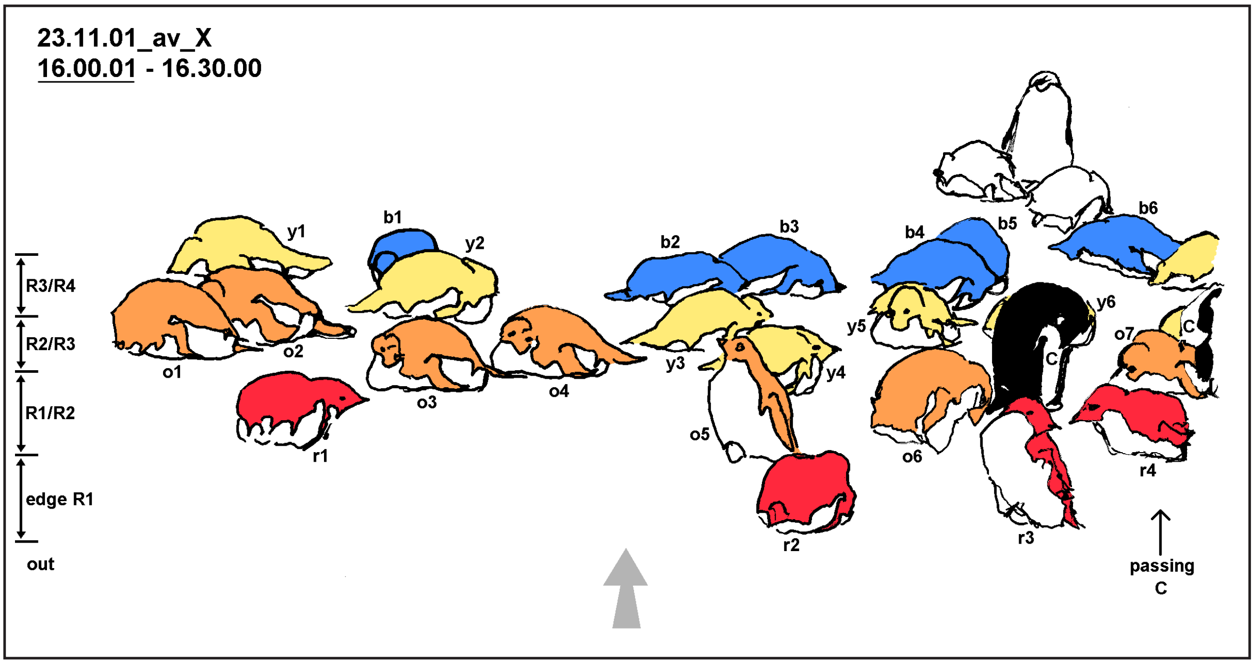

Figure 4-12: Areas Delineated for Focal-Group Primary Transcription of Conspecific Presence. Double-headed arrows indicate between-row areas used for transcription of sessions recorded at group X. The grey arrow depicts direction from which visitors approached. C: conspecifics currently not engaged in incubation; rows were differently coloured for better discrimination, and nest codes reflect colours used (r: red = R1, o: orange = R2, y: yellow = R3, b: blue = R4).

As regards focal animals, three concentric zones of increasing area were designated round the focal penguin's nest (concept 'borrowed' from Nimon 1997). Zone 'a' comprised the area immediately surrounding the focal penguin's nest up to the nearest neighbouring nests, zone 'b' the area between one and two nests away, and zone 'c' the area between two and three nests away from the focal penguin (fig. 4-13). These zones continued beyond the colony edge.

Duration of exposure to the disturbance: Conspecifics moved and stood unrestrained. Due to sampling method (Instantaneous-Scan Sampling), time of exposure did not feature with respect to focal groups. As regards focal animals, time of presence of conspecifics was separately noted in the three nest zones of increasing distance from the focal animal (fig. 4-13).

4.3.4.2.3 Predator/ Aircraft Disturbance

Due to their rare occurrence, disturbances by predators as well as by aircraft noise were sampled ad libitum. This information was not systematically evaluated and did not receive any operationalisation. With respect to **predators**, however, species, approximate height of overflight (high, medium, and low) and occurrences of presence on ground were noted whenever possible. The rare instances of **aircraft** 'presence' were noticed by noise, not visual appearance; a distinction between helicopter and plane was not feasible.

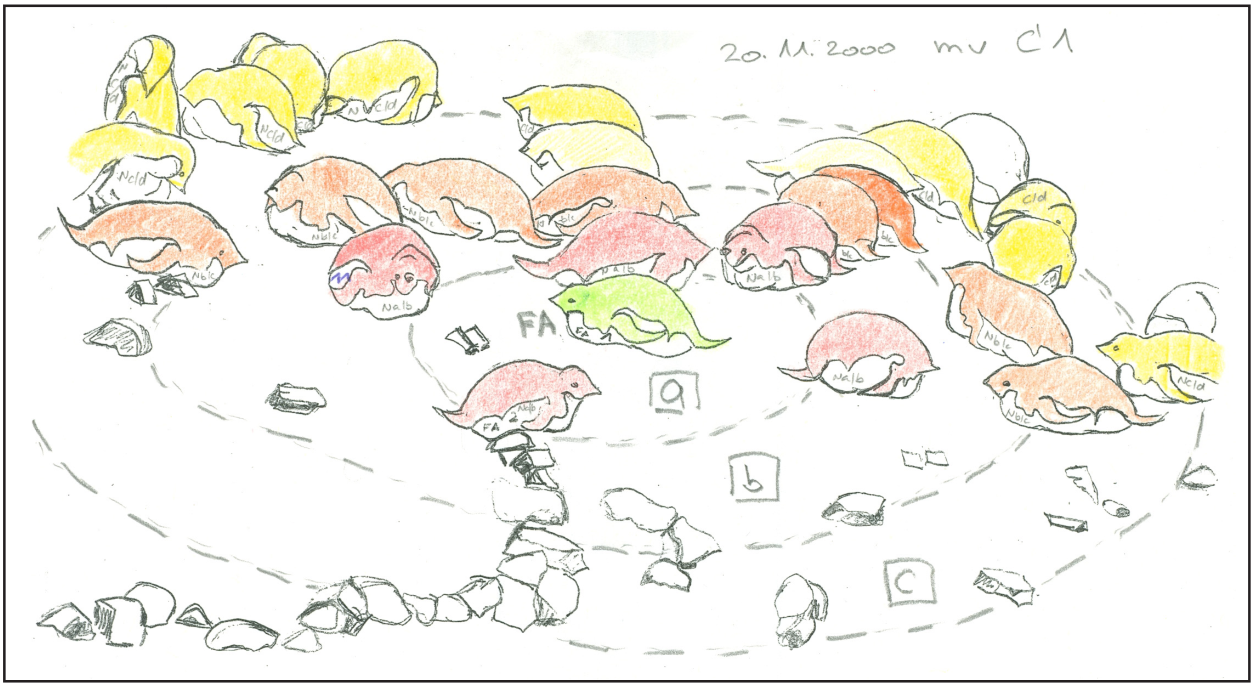

Figure 4-13: Nest Zones Delineated for Focal-Animal Primary Transcription of Conspecific Disturbance. The sketch depicts nest zones drawn around focal animal C1-1. FA: focal animal, N: neighbour; a, b, c: concentric nest zones of increasing distance from focal nest in centre.

4.3.4.3 Focal Groups: Primary Transcription of Disturbance

4.3.4.3.1 Human Disturbance

For each sampling point, the **number** of humans (none, 1 P, 3 P), their **conduct** (if present: loud and fast vs. silent and slow) and their **distance** from the colony edge (not present before, 15 m, 5 m, 3 m, retreat, not present after; approaching to respective distances) were noted on the primary transcription sheets.

4.3.4.3.2 Conspecific 'Disturbance'

For each sampling point, the **number** of conspecifics and their respective **positions** in six separate areas were noted (fig. 4-12). These areas depended on focal-group 'boundaries' and comprised the categories 'outside colony', at the 'colony edge', and within or between the respective rows.

N.b.: For group evaluations, only the **presence** of conspecifics was noted. **No** distinctions were made according to the conspecifics' **conduct** (e.g. standing, walking past, approaching nests, interacting with breeding birds etc.).

4.3.4.3.3 Predator/ Aircraft Disturbance

Predator presence was entered in the 'remarks'-column of the primary (hard-copy) transcriptions (see exemplary matrix in appendix 4-2). Generally, this referred to **Skuas** (*Catharacta* spp.) or **Southern giant petrels** (*Macronectes giganteus*). Skuas[60] were either flying low across the colony (skua low overflight, SLOF) or landing at or close to the colony edge (skua on ground). If overflights occurred at a greater height (high/ medium overflight, HOF/ MOF), the video tape captured only the **shadow** of a bird passing across the colony so that it was impossible to determine the species.

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[60] Within the zones relevant for transcription, Giant petrels were not observed on ground or performing low overflights.

Passing shadows were also entered in the hard-copy transcription whenever they were clearly visible on the video[61] .

Aircraft noise emanating from helicopters or planes was likewise noted in the ‘remarks’-column (time of beginning and end) whenever the noise was audible on tape or had been noted at the time of recording.

4.3.4.4 Focal Groups: Outlook on Secondary Transcription of Disturbance

In line with behaviour sampling methods (ISS, OZS), the **performance indicator values** calculated represented disturbance at a given sampling point (every 30 s). These values were entered into Excel and SPSS matrices for correlation with focal-group behaviour/ posture.

Recapitulation: Details are provided in the **methodological prelude** at the beginning of chapter 5.1.1. A schematic overview of steps involved in data processing (transcriptions, analyses, and visualisation) is found at the end of this chapter (4.5, tab. 4-23).

4.3.4.4.1 Human Disturbance

The Point Performance Indicator Value for Human Visitation (PPIV-H) was used to reflect changes in intensity of human disturbance. It constituted a **weighted** measure, integrating visitor distance, number and conduct at each sampling point.

4.3.4.4.2 Conspecific ‘Disturbance’

The Point Performance Indicator Value for Conspecific Presence (PPIV-C) simply reflected changes in total number of conspecifics present at a given sampling point (from ‘out’ to ‘between 4th and 5th row’). It represented an **unweighted** measure, i.e., conspecific movement and conduct were not taken into account.

4.3.4.4.3 Predator/ Aircraft Disturbance

Ad libitum sampling notations in the ‘remarks’-column of primary transcriptions were entered into a corresponding column in the Excel matrices. They did not receive a separate evaluation, but were used to exclude certain data points from analyses of responses to human or conspecific disturbance (missing data, q.v.) prior to entry into the corresponding SPSS-matrices.

4.3.4.5 Focal Animals: Primary Transcription of Disturbance

Reflecting the ‘sampling’ method (All-Occurrences Sampling), primary transcription of disturbance for focal-animal evaluations was effected at a higher resolution (second-by-second) than for focal groups.

4.3.4.5.1 Human Disturbance

The exact times during which the focal animal was subjected to human visitation (time of approach, time spent at each of the three distances, time of retreat), number of human visitors present and the behaviour they exhibited were transferred to the ‘remarks’-column of the primary transcription sheets (hard-copy).

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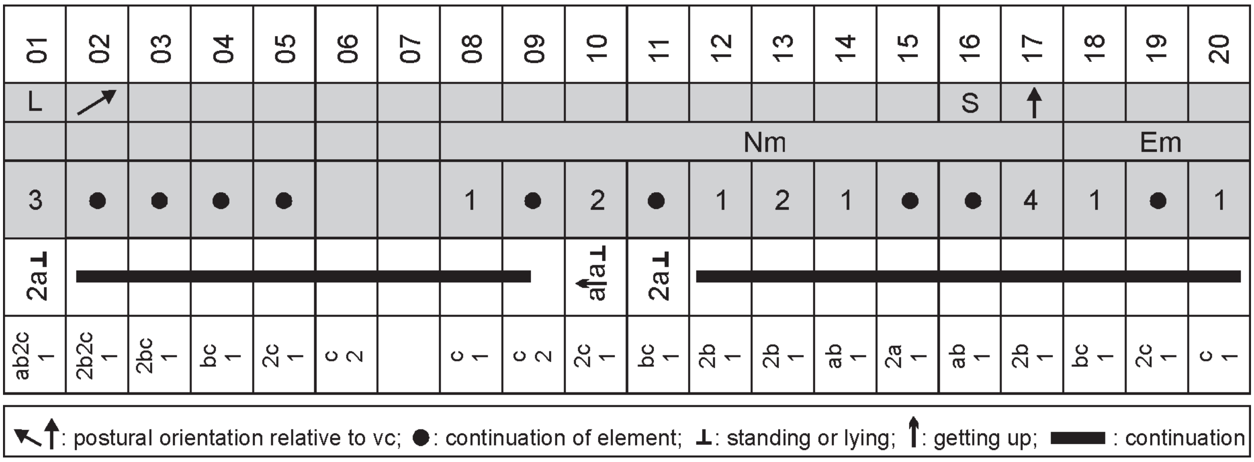
[61] Visibility depended on height of overflights of the birds throwing the shadows as well as on light and wind conditions.

4.3.4.5.2 Conspecific Disturbance

Conspecifics were grouped[62] according to current speed of movement[63] (standing/ lying, walking, running) within each of the three concentric nest zones (see fig. 4-13). Additionally, selected aspects of conspecific behaviour (e.g., fights, nest stone thefts at the focal animal's nest) were noted. In the primary transcription sheet, second-by-second information on conspecifics was entered below transcription notes of focal-animal behaviour and posture (fig. 4-14).

N.b.: During fights and nest stone thefts, as well as while getting up, otherwise stationary conspecifics were defined as moving. Details on transcription rules are found in appendix 4-1.



01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20
L	↗														S	↑			
							Nm										Em		
3	●	●	●	●			1	●	2	●	1	2	1	●	●	4	1	●	1
2a⊥	▬								a↑a⊥	2a⊥	▬								
ab2c 1	2b2c 1	2bc 1	bc 1	2c 1	c 2		c 1	c 2	2c 1	bc 1	2b 1	2b 1	ab 1	2a 1	ab 1	2b 1	bc 1	2c 1	c 1

↖↑: postural orientation relative to vc; ●: continuation of element; ⊥: standing or lying; ↑: getting up; ▬ : continuation

Figure 4-14: Example of 20 s of Primary Transcription of Conspecific Data. Grey-shaded rows (2 to 4) repeat entries of primary (q.v.) transcription of focal-animal behaviour and posture, unshaded rows depict notes with respect to conspecifics. Row one represents time (s), rows five and six provide information on stationary and moving conspecifics, respectively. Numbers before letters represent number of conspecifics in each nest zone (no number = 1 individual in each zone mentioned), numbers behind last letters denote speed (1 = walking, 2 = running). a, b, c: conspecifics in three nest zones; upper row: standing/ lying conspecifics, bottom row: moving conspecifics.

4.3.4.5.3 Predator/ Aircraft Disturbance

Onset and duration of occurrences of predator presence as well as aircraft noise were entered into the 'remarks'-column of the primary transcription sheet.

4.3.4.6 Focal Animals: Outlook on Secondary Transcription of Disturbance

Secondary transcription of disturbance was performed to align focal-animal parameters (behaviour, posture, and heart rate) and disturbance parameters. Secondary transcriptions reflected the **different foci** employed during analyses of behaviour ELEMENTS and of behavioural TOPOGRAPHY, respectively.

During evaluations of behaviour *ELEMENTS*, posture and heart rate, the focus was on the 'disturbees' (the incubating penguins, i.e. FAs), and transcription of disturbance was adapted to the time frame chosen to analyse the focal animals' comportment (20 s-intervals, primarily opted for due to duration of heart rate counting-intervals).

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[62] N.b.: No attempt at individual recognition was made. Grouping was solely based on shared characteristics during a given second, e.g., three conspecifics moving in nest zone b.

[63] In contrast to human visitation, the noise level (i.e., loud vs. silent) was impossible to discern due to distance between camera microphone and colony.

The resulting Interval Performance Indicator Values for Human Visitation (IPIV-H) and Conspecific Disturbance (IPIV-C) thus constituted measures additionally weighted by time of exposure per 20 s-interval (s.b., tabs. 4-17 and 4-18).

With respect to behavioural, postural and heart rate *TOPOGRAPHY*, the ‘disturbing agents’ (humans, conspecifics) were focused upon, and focal-animal comportment (behaviour, posture, and heart rate) was evaluated within disturbance time frames (s.b.).

4.3.4.6.1 Human Disturbance

ELEMENTS: Human visitation was categorised according to a combination of visitor conduct (type), number of visitors (one or three), time of presence (in seconds) of visitor(s) at a given distance (15 m, 5 m, 3 m), and movement towards (approach) resp. away from (retreat) the penguins (tab. 4-17).

Total human disturbance was represented by the Interval Performance Indicator Value for Human Visitation (IPIV-H). IPIV-H was calculated by summing up the weighted values assigned to each of these components per 20 s-interval (tab. 4-17). Performance indicator values were entered into the secondary transcription matrix for statistical analyses.

Example:

In a given 20 s-interval,
1 person (1 P = *2*)
performing a ‘loud and fast’ visit (L&F= *4*)
spent 8 s at 5 m (H_b = *4*),
then approached to 3 m (= *3*),
and stayed there for the rest of the interval, 12 s[64] (H_a = *12*).

The resulting **IPIV-H** adds up to 25. IPIV-H values ranged from 5 to 36[65].

TOPOGRAPHY: Visual appraisal of impact of human disturbance was undertaken separately for each visiting stage characterised by the Visiting Stage Performance Indicator Value (VS-PIV). Visiting stages and their respective performance indicator values are shown in table 5.3.1-3 (chapter 5.3.1.1).

4.3.4.6.2 Conspecific Disturbance

ELEMENTS: Conspecific disturbance was categorised integrating speed of movement, selected aspects of behaviour, number, and time of presence (duration in seconds) at three different distances from the focal animal’s nest (fig. 4-13). Total conspecific disturbance was represented by the Interval Performance Indicator for Conspecific Disturbance (IPIV-C). IPIV-C was calculated by summing up the weighted values assigned to each of the components per 20 s-interval (tab. 4-18). Interval performance indicator values were entered into the secondary transcription matrix for statistical analyses.

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[64] Note that approach time to a given distance counted towards time spent at that distance, but received the additional weighting.

[65] IPIV-H = 36 results if 3 P (*4*), L&F (*4*) spend no time in H_c (*1*), 4 s in H_b (*4*), approach to H_a (*3*), and spend 16 s in H_a (*20*).

Table 4-17: Interval Performance Indicator Value for Human Disturbance (IPIV-H) Used in Evaluations of Focal-Animal Behaviour Elements, Posture, and Heart Rate. IPIV-H was calculated per 20 s-interval by adding the absolute values for visitor (conduct, number) and dynamic distance components (approach) to duration-dependent values for static distance components. S&S: silent and slow, L&F: loud and fast; 1 P: one visitor, 3 P: three visitors; H_: visitor(s); approach, at 15 m/ 5 m/ 3 m, retreat: stages of the visit. Similar to conspecific disturbance, the three distances were coded as 'a' (3 m), 'b' (5 m), and 'c' (15 m).

Visitor Components				Distance Components						
				Dynamic		Static				
H_conduct	Matrix entry	H_number	Matrix entry	H_approach	Matrix entry	Seconds (per 20 s-interval)	Matrix entry for 00 s-02 s	Matrix entry for 03 s-08 s	Matrix entry for 09 s-14 s	Matrix entry for 15 s-20 s
unvisited	1	unvisited	1	to 15 m	1	visitor(s) at 15 m (H_c)	1	2	3	5
S&S	2	1P	2	to 5 m	2	visitor(s) at 5 m (H_b)	1	4	6	10
L&F	4	3P	4	to 3 m	3	visitor(s) at 3 m (H_a)	1	8	12	20
H_retreat (S&S): add 4 s to sum H_a, and 6 s to sum H_b [= average time at (s)low speed]						Visitor waves arms in distance a: add 2 to IPIV-H (occurred only at 1P, L&F)				
H_retreat (L&F): add 2 s to sum H_a, and 4 s to sum H_b [= average time at high speed]						Visitor waves arms in distance b: add 1 to IPIV-H (occurred only at 1P, L&F)				
Interval Performance Indicator Value for Human Visitation (IPIV-H) = sum of matrix entries (H_conduct, H_number, Hc, Hb, Ha, if applicable H_wave) per 20 s-interval										

Table 4-18: Interval Performance Indicator Value for Conspecific Disturbance (IPIV-C) Used in Evaluations of Focal-Animal Behaviour Elements, Posture, and Heart Rate. IPIV-C was calculated by weighting number of conspecifics according to conduct for every second, subsequently adding these separately for each nest zone (c, b, a) per 20 s-interval, looking up the corresponding figure (matrix entry), and finally summing up figures of all three nest zones. **N.b.:** Only selected examples are given with respect to conspecific conduct; the complete list is provided in appendix 4-1. C: conspecific; n C: any number of conspecifics in a given nest zone and second; fight: includes body/ bill contact, dispute: no body/ bill contact involved (point, gape; q.v.); FA: focal animal.

movement components				distance components				
C_conduct per second	weighting factor	C_number per second	weighting factor	figure (per 20s-interval)	Matrix entry for sum = 0-2	Matrix entry for sum = 3-8	Matrix entry for sum = 9-14	Matrix entry for sum = 15 and above
walk run	1 2	1 C	1	conspecifics in nest zone c (C_c)	1	2	3	5
dispute fight (with FA)	2 3	2 C	2	conspecifics in nest zone b (C_b)	1	4	6	10
C gets up	in c: 1 in b: 2 in a: 3	n C	n	conspecifics in nest zone a (C_a)	1	8	12	20
Interval Performance Indicator Value for Conspecific Disturbance (IPIV-C) = sum of number of conspecifics (weighted by conduct) in each distance (C_c, C_b, C_a) per 20 s-interval								

01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	
2a⊥	▬	▬	▬	▬	▬	▬	▬	▬	↑a⊥	2a⊥	▬	▬	▬	▬	▬	▬	▬	▬	▬	
ab2c 1	2b2c 1	2bc 1	bc 1	2c 1	c 2		c 1	c 2	2c 1	bc 1	2b 1	2b 1	ab 1	2a 1	ab 1	2b 1	bc 1	2c 1	c 1	**sum**
2	2	1	1	2	2		1	2	2	1							1	2	1	**20**
1	2	2	1							1	2	2	1		1	2	1			**16**
1									3				1	2	1					**8**

⊥ : standing or lying; ↑: getting up; ▬ : continuation.

Figure 4-15: Example of 20 s of Secondary Transcription of Conspecific Data. Grey-shaded rows repeat entries of primary (q.v.) transcription of conspecific numbers and conduct, unshaded rows depict time (s; first row) and calculations for conspecifics in nest zones c (upper = fourth), b (middle = fifth), and a (lower = sixth row) towards the Interval Performance Indicator Value for Conspecific Disturbance (IPIV-C). In the grey rows, numbers before letters represent number of conspecifics in each nest zone, numbers behind last letters denote speed (1 = walking, 2 = running). a, b, c: conspecifics in three nest zones; upper row (second): standing/ lying conspecifics, bottom row (third): moving conspecifics.

Example:

1. Conspecific disturbance is summed up in each of the three nest zones (fig. 4-15):

   nest zone c: 16 (walking) + 4 (running) → **20**

   nest zone b: 16 (walking) → **16**

   nest zone a: 5 (walking) + 3 (1 bird in zone ‘a’ getting up) → **8**

   Stationary conspecifics do not count unless they ‘move’ (e.g., getting up)

2. Next, the respective sums are converted into matrix entries (tab. 4-18):

   nest zone c: 20 → **05**

   nest zone b: 16 → **10**

   nest zone a: 08 → **08**

The resulting **IPIV-C** adds up to 23.

TOPOGRAPHY: Numbers of conspecifics were summed up for 10 s-intervals. While disregarding behaviour (fights, nest stone thefts, etc.), distinction was made between stationary (summed up for nest zone a, ‘ignored’ in zones b and c) and moving conspecifics. Within the latter, conspecifics moving in nest zones a, b, and c were summed up separately. Impact of conspecific disturbance was subsequently appraised by looking at focal-animal responses to increased conspecific **movement** (regardless of distance; in nest zone a) and conspecific **stationary presence** (only in nest zone a) **outside human visitation**. Both periods (i.e. before and after visitation) were examined conjointly, as preliminary comparisons between responses to conspecifics pre- and post-visit did not reveal any differences with respect to consistency (response yes/ no) which was of interest at that level of evaluation (key question: How many birds do respond?).

Prior to visitation, the Conspecific Movement Measure (tab. 5.3.1-4, chapter 5.3.1.1) gauged extent and consistency of conspecific **movement** per 2 min interval.

4.3.4.6.3 Predator/ Aircraft Disturbance

Onset and duration of occurrences of predator presence as well as aircraft noise were entered into the ‘remarks’-column of the secondary transcription sheet. They were not included in statistical analyses, but featured in qualitative assessments of focal-animal responses, e.g., during visual appraisal.

4.3.4.7 Missing Data

Visitor location was accounted for at all times so that there were no missing data for this parameter. Data on **conspecifics** usually went missing along with focal-animal/ focal-group behaviour data. Consequently, no specific rules had to be devised.

As stated above, **predator presence** and **aircraft noise** were not sampled systematically so that the term ‘missing data’ does not strictly apply. During analyses, however, these encounters were deliberately left out in certain circumstances, effectively resulting in missing data. When analysing penguin (group) reactions to human visitation and/or conspecific presence, for instance, it was necessary to exclude those samples in which reactions were most likely to have been caused by predator or aircraft disturbance:

For focal-group analyses, ‘penguin data points’ acquired during the presence of predator(s) or aircraft noise were thus **excluded** from evaluations if values for the whole group differed markedly (being at least twice as high/ low) from values immediately before and after.

Focal-animal analyses of behaviour *ELEMENTS*, posture, and heart rate followed a similar approach in that a 20 s-interval in which these disturbances had been noted was **excluded** if its contents differed markedly from the previous interval. The following intervals were likewise excluded until values returned to pre-disturbance level.

Concerning quantitative analyses of *TOPOGRAPHY* of behaviour, posture and heart rate, it was considered impractical to eliminate data obtained during brief outbursts of predator presence/ stretches of aircraft noise, particularly with respect to phase/ state durations. Instead, encounters were marked in the topography charts, and these types of disturbance were examined qualitatively during pre- and post-visit stretches of behaviour/ heart rate. In the section summary, consistency of focal-animal response to those disturbance types is presented and compared to responses observed towards human visitors and conspecifics (see chapter 5.3.1.13).

4.4 Data Analyses

Excel matrices (Microsoft 1997, 2003) were used for ‘simple’ calculations (e.g., proportions) and the generation of various graphs. Additionally, a specially designed Excel matrix served to calculate partial correlations. The remaining statistical analyses were performed using SPSS (Releases 10.0-14.0, correlations), and SYSTAT (Release 1.2; Friedman-tests).

4.4.1 Calculation of Performance Indicator Values, Indices, and Proportions

4.4.1.1 Focal Groups and Focal Animals: Performance Indicator Values (PIVs)

Performance Indicator Values were devised to relate disturbance to focal-group (behaviour, posture) and focal-animal (behaviour, posture, heart rate) comportment.

For **focal groups**, Point Performance Indicator Values (PPIVs) represented the weighted sum of human visitation and unweighted sum of conspecific presence, respectively, calculated every 30 s (Instantaneous-Scan Sampling interval).

As regards focal animals, Interval Performance Indicator Values (IPIVs) captured the weighted sum of human visitation/ conspecific disturbance calculated for each 20 s-interval during evaluations of ‘**focal-animal elements**’ (behaviour, posture, and heart rate).

With respect to visual appraisal of ‘**focal-animal topography**’ (behaviour, posture, and heart rate), the Visiting Stage Performance Indicator Value (VS-PIV) served to visually distinguish different stages of human visitation. Additionally, the Conspecific Movement Measure (CMM) was used to gauge extent and continuity of conspecific movement per 2 min-interval prior to visitation.

PIVs and the CMM have been introduced above (see sections on Secondary Transcription of Disturbance in this chapter), and details on calculations will be provided in the respective results chapters.

4.4.1.2 Focal Groups: ‘Penguin Unit’-Index for Period Differences and Row Differences

To render group reactions comparable across periods and sessions, as well as between different rows and groups, **‘penguin unit’-indices** (PUI-R, PUI-G) were calculated (chapter 5.1.1). The indices corrected for differences in number of sampling units (points or intervals) and differences in the number of penguins per group or row (within groups or rows across different sessions, as well as between different groups or rows).

The procedure resulted in values ranging from 0.00 to 1.00, with larger values indicating a greater proportion of penguins assigned to the respective category.

4.4.1.3 Focal Animals: Behaviour Elements, Posture, and Heart Rate – Rates and Durations

For focal-animal behaviour element analyses, all data (rates, durations) were computed per 20 s-interval. Detailed rules with respect to focal-animal **behaviour/ posture** are presented in appendix 4-1. In conjunction with analyses of behaviour elements/ posture, **heart rate** was counted for 20 s and extrapolated to beats per minute values.

4.4.1.4 Focal Animals: Behavioural, Postural, and Heart Rate Topography – Proportion of Phases/ States

The number and duration of phases (categorised behaviour systems; heart rate categories) and states (posture categories) was examined for each period (pre-visit, during-visit, post-visit).

For comparison of distributions of observed **phase/ state durations** between behaviour systems/ postures/ heart rate categories, and across periods, **proportions** were calculated (see chapter 5.3.3).

4.4.2 Statistical Analyses

4.4.2.1 Descriptive Statistics

4.4.2.1.1 'Averaging' Information

For **focal-group behaviour and posture**, the **arithmetic mean** (plus standard deviation[66]) was used whenever data of the same dataset (i.e., B_1, B_2, C_1, C_2, X, Y)[67] were averaged (across sessions or rows, e.g. in graphs). When depicting mean values for all datasets (e.g., in statistical tables), the **median** (plus range) was additionally provided. Constituting a 'central value' more resilient with respect to outliers, the median was considered more adequate for representation of 'overall average'; while the range ensured that between-group differences were kept firmly in mind.

As for **focal-animal behaviour, posture and heart rate**, the between-session differences found in individual focal animals, as well as the extent of differences found among sessions recorded from different individuals on the same day, were considered sufficiently large to warrant calculation of proportions **without** prior averaging of information. While this practice is arguable, it prevents the loss of information on naturally occurring variation within each focal animal and within each day.

During **Visual Appraisal** (q.v.), **mean period values** (before, during, after human visitation) were calculated to assess whether these adequately reflected responses observed in each of a number of shorter intervals (for pre- and post-visitation: 2 min-intervals; for during-visitation: visiting stages).

With respect to **focal-animal heart rate**, **mean values** were employed in two cases:

Mean resting heart rate (RHR, q.v.) was determined by taking the mean of pre-visit 20 s-values of heart rate obtained during the behaviour system of rest.

During brief stretches of signal obfuscation (q.v.), the mean between legible heart rate prior to and after illegible heart rate was used to calculate the missing part in-between.

4.4.2.1.2 Boxplots

Boxplots (depicting minimum, 1st quartile, median, 3rd quartile and maximum values) were used to visualise differences in behaviour and posture between periods (pre-visit, during-visit, post-visit), as well as between groups subjected to different visiting schemes (during-visit).

Variation in these statistical parameters (as well as in mean, standard deviation, and range) was also used to characterise heart rate variation before, during, and after human visitation.

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[66] not shown in pie charts

[67] group A did not form part of focal-group evaluations

4.4.2.2 Univariate Inference Statistics

4.4.2.2.1 Kolmogorov-Smirnov Goodness-of-Fit-Test

Kolmogorov-Smirnov Goodness-of-Fit-tests indicated that data were generally not normally distributed ($p >> 0.05$). Therefore, **all tests** in THIS THESIS are **non-parametric**.

4.4.2.3 Bi- and Multivariate Inference Statistics

The statistical literature is replete with arguments in favour of as well as against the usage of particular methods in particular circumstances. The following section thus briefly accounts for the procedures employed in THIS THESIS.

4.4.2.3.1 Spearman's Rank Correlations

Spearman's rank correlation coefficient is a non-parametric measure of correlation, i.e., it assesses how well an arbitrary monotonic function could describe the relationship between two variables, without making any assumptions about the frequency distribution of the variables. The coefficient is denoted by the Greek letter ρ_s (*rho*$_s$) when the population is referred to or given as r_s where the sample is concerned. Concerning samples, r_s is identical to the [parametric] product-moment-correlation if both variables assume values between 1 and n; a condition that applies to ranks.

In principle, r_s is thus simply a special case of the Pearson product-moment coefficient in which the data are converted to rankings before calculating the coefficient. Unlike the Pearson product-moment correlation coefficient, however, it does not require that the relationship between the variables is linear, nor does it require the variables to be measured on interval scales; it can be used for variables measured at the ordinal level (i.e., ranks). According to BORTZ (1999), it was MARX (1981/ 1982) who demonstrated that Spearman's ρ constitutes a viable statistic for ordinal scales.

Spearman's rank correlations were calculated during **focal-animal analyses** to examine relationships between selected behaviour elements and heart rate.

Furthermore, concerning **focal-animal** and **focal-group analyses**, 'unadjusted' rank correlations were calculated between disturbance parameters (human visitation, conspecific disturbance) and behaviour elements of focal animals, between disturbance parameters (human visitation, conspecific disturbance) and heart rate of focal animals, and between disturbance parameters (human visitation, conspecific presence) and aspects of focal-group behaviour.

4.4.2.3.2 Partial Rank Correlations

> "With more than two variables, you often want to know the correlation between *x* and *y* when a third variable, say *z*, is held constant. The partial correlation coefficient measures this. It enables correlation due to a shared common cause to be distinguished from direct correlation." (CRAWLEY 2007, p. 96)

According to BORTZ & LIENERT (2003), a specific procedure for partial rank correlations has not been developed yet. Assuming that the linear relationships between three variables X, Y and Z are estimated with sufficient exactitude by the rank correlations $r_{s(xy)}$, $r_{s(xz)}$ and $r_{s(yz)}$, the partial rank correlation can be determined as follows[68] :

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[68] transl. K. SCHUSTER

Equation 4-1

$$\boxed{r_{s(xy\bullet z)} = \frac{r_{s(xy)} - r_{s(xz)} \times r_{s(yz)}}{\sqrt{1 - r_{s(xz)}^{2}} \times \sqrt{1 - r_{s(yz)}^{2}}}}$$

N.b.: The dot separating *z* from *x* and *y* is the mathematical way of telling the reader that *z* is the variable to be partialled out.

The partial rank correlation can be approximately[69] tested for significance in the same manner as the parametric partial correlation[70]:

Equation 4-2

$$\boxed{u = Z \times \sqrt{N - 4}}$$

u = value on x-axis (= Abszissenwert)

Z = Fisher's Z-value

N = number of cases

Usage of equation 4-2 necessitates transformation of the calculated partial correlation coefficient (which is invariably positively defined) into a so-called Fisher's Z-value. For this, a specific transformation table is used (e.g., table V in the appendix of Bortz & Lienert 2003). The resulting *u*-value is subsequently compared with a critical value[71], which can be found in another table frequently listed in statistic textbooks (e.g., obtained from table A in the appendix of Bortz & Lienert 2003)[72]: The corresponding *p*-value constitutes the exceeding probability for abscissa-values/ *u*-values of the standard normal distribution.

With respect to **focal groups**, partial rank correlations were calculated to 'separately examine' the influence of each of the two sources of disturbance during visitation, viz., human and conspecific, on the group behaviour recorded.

4.4.2.3.3 Coefficient of Determination (R^2)

> "Die Korrelation wird mit *r* und der Determinationskoeffizient mit R^2 bezeichnet. Es besteht im bivariaten Fall in der Tat genau diese Beziehung zwischen den beiden, dass der Determinationskoeffizient das Quadrat der Korrelation ist." (Müller-Benedict 2007, p. 259)[73]

In statistics the coefficient of determination R^2 represents the proportion of variability in a given data set that is accounted for by a statistical model. R^2 is interpreted as the proportion of response variation (variance found in dependent variable) 'explained' by the regressors (variance found/ experimentally induced in independent variables) in the model. Thus, an R^2-value of 1.0 indicates

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[69] for German readers: 'näherungsweise'

[70] transl. K. Schuster

[71] transl. Dr. A. Reuss

[72] transl. K. Schuster

[73] Correlation is denoted by *r*, and the coefficient of determination by R^2. In bivariate statistics, that is exactly the relationship between the two, viz., the coefficient of determination is the correlation squared. (transl. K. Schuster)

that the fitted model explains all variability in y (dependent variable), while the term $R^2 = 0.0$ indicates that no 'linear' relationship between the response variable and regressors exists. Any intermediate value, e.g., $R^2 = 0.7$, may be interpreted as follows: Approximately seventy percent of the variation in the dependent (response) variable can be explained by the independent (explanatory) variable. The remaining thirty percent are due to unknown variables or inherent variability. According to Müller-Benedict (2007, see quote), the interpretation of r^2 is the same as that of R^2 in bivariate statistics (proof is given in Müller-Benedict 2007, p. 259).

In this thesis, r^2- rather than r-values are presented to facilitate interpretation of the obtained results; r^2-values emphasise that whenever r is doubled, its explanatory power is quadrupled.

Example:

Response FA 1 to conspecific disturbance, $r = 0.4$ → $r^2 = 0.16$ = 16 % of variance explained.

Response FA 2 to conspecific disturbance, $r = 0.8$ → $r^2 = 0.64$ = 64 % of variance explained.

4.4.2.3.4 Colour Codes for Correlations

Spearman's rho correlation coefficients (r_S) have been transformed to r^2-values. These values are categorised and interpreted adapting Sprinthall's suggestions for correlations (1987, quoted in Martin & Bateson 1993). To facilitate visual discrimination, the categories were colour-coded. Table 4-19 shows the categories and their respective colour codes.

Table 4-19: Colour Codes for and Informal Interpretation of r^2-Values, Modified Following Sprinthall (1987).

5	**0.810 ? r^2 < 1.000**	**very high** correlation, very dependable relationship (not in these datasets)
4	0.490 ? r^2 < 0.810	**high** correlation, marked relationship
3	0.160 ? r^2 < 0.490	**moderate** correlation, substantial relationship
2	0.100 ? r^2 < 0.160	**low** correlation, definite but small relationship
1	0.001 ? r^2 < 0.100	**slight** correlation, almost negligible relationship

With respect to categories 3-5, interpretation followed Sprinthall (1987), the bottom threshold for category 'low', however, was more conservatively set at 0.100 (i.e. explaining 10 % of the variance, instead of 4 % as calculated from Sprinthall's $r_S < 0.2$).

4.4.2.3.5 Friedman-Test

Friedman-test is a non-parametric statistical test. Similar to the parametric Repeated Measures ANOVA[74] , it is used to detect differences in treatments across multiple tests. The Friedman-test is used for two-way repeated measures analysis of variance by ranks. According to Diehl & Staufenbiel (2001), the Friedman-test constitutes an extension of the Sign-test[75] (to which it is approximately equivalent whenever only two groups are examined), as it permits a comparison of more than two groups. In contrast to the Sign-test, however, the Friedman-test accounts for ties (equal values). Box 4-4 outlines the test procedure.

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[74] ANalysis Of VAriance

[75] Sign-test for dependent samples is employed to test whether in a set of paired values (i.e. two groups) those measured under condition B (e.g., at point in time t2) deviate significantly from those measured under condition A (e.g., at point in time t1). Ties are ignored.

Box 4-4: Friedman-Test – Procedure. T^{mean}: mean rank; j, j’: two dependent samples; $D_{Tmean\ crit}$: critical difference suitable for comparison of rank-means of two dependent samples; df: degrees of freedom.

$$\left|\mathbf{T}^{\mathbf{mean}}_{\mathbf{j}} - \mathbf{T}^{\mathbf{mean}}_{\mathbf{j'}}\right| = \mathbf{D}_{\mathbf{Tmean\ crit}}$$

To be significant, the absolute value of ‘mean rank $\mathbf{T}_j$ minus mean rank $\mathbf{T}_{j'}$’ must be equal to or larger than the critical difference of the rank-means.

The critical difference of the rank-means is calculated using the following equation:

equation 4-3 $$^{\#}\mathbf{D}_{\mathbf{Tmean\ crit}} = \sqrt{\chi^2_{crit} \bullet \frac{k*(k+1)}{6*N}}$$

k equals the number of treatment-types (e.g., penguins nesting in different rows)

6 is a fixed number

N equals the number of groups (e.g., sessions)

χ^2_{crit} is the critical threshold-value for a previously set α-level (e.g., 2-tailed $p = 0.05$, df = 3)

N.b.: χ^2_{crit} is found in tables of statistics books, e.g. in Bortz & Lienert (2003):

Table I (p. 389) for **exact** exceeding probabilities[##], **Table B** (p. 360) for **asymptotic** exceeding probabilities.

[#] equation in Bortz & Lienert (2003, p. 190)

[##] exceeding probabilities = Übertretungswahrscheinlichkeiten

In **focal-group analyses**, Friedman-test was performed to examine whether differences in the behaviour of penguins nesting in different rows of increasing distance from human disturbance were statistically significant. In case of significant results, pair-wise Friedman-tests (and sequential Bonferroni adjustments, q.v.) were calculated to detect between which rows the significant difference existed.

In **focal-animal analyses** of **topography**, the Friedman-test was used to examine consistency of directions of change between periods (pre-, during-, and post-visitation) for all focal animals together.

4.4.2.3.6 Colour Codes for Significance Levels

Unless mentioned otherwise, **all *p* are two-tailed**. For exploratory significance testing, different levels of significance were colour-coded. Table 4-20 shows the levels and their respective colour codes.

Table 4-20: Colour Codes for Significance Levels for α_F = Overall Significance.

4	$0.0001 \le p < 0.001$	very highly significant
3	$0.001 \le p < 0.01$	highly significant
2	$0.01 \le p < 0.05$	significant
1	$0.05 \le p < 0.1$	tendentially significant

4.4.2.3.7 Adjustment of α-Error Level

Multiple follow-up pair-wise comparisons (i.e., pair-wise comparisons conducted 'in the wake of' a global test) bear the burden of an inflated α-error level. Adjustment helps to keep the α-error at the fixed overall level, thereby avoiding an increase in the probability of an unjustified rejection of H_0. As, however, adjustment of the α-level is unfortunately complemented by a decrease in power, usage is far from universally recommended (e.g., COHEN 1992; MORAN 2003; NAKAGAWA 2004; PERNEGER 1998). With respect to multiple hypothesis testing in general, COHEN (1992, p. 156) suggests that "in studies testing several H_0s, it is recommended that α = 0.01 per hypothesis in order that the experimentwise risk (i.e., the risk of any false rejections) not become too large".

Concerning the adjustment procedure, several methods are available.

In the **'simple' Bonferroni adjustment**, α is (simply) divided by the number of pair-wise comparisons performed.

'Simple' Bonferroni-adjustment: α **divided by the number of pair-wise comparisons**

α_F (alpha on the 'family-level[76]') → α_V (alpha on the 'level of variables[77]')

Example:

At a significance level of **alpha**$_F$ = 0.05 and six comparisons,
the Bonferroni-adjusted significance **alpha**$_V$ equals $0.05 * {}^1/_6 = 0.008333\ldots$

BORTZ (1999, p. 261[78]), however, states that the 'simple' Bonferroni adjustment of the α-error tends to be conservative, i.e. the adjustment tends to be 'somewhat stricter than strictly necessary'. Furthermore, the author points out that α-error adjustments like the one developed by Bonferroni assume orthogonal (independent) data[79].

A **sequential approach** to adjusting the α-error is suggested by HOLM (1979; this procedure is also referred to as 'Holm's sequential Bonferroni' or 'Holm-Bonferroni method'). It consists of arranging the *p*-values of the pairwise tests by magnitude, starting with the lowest value, and then checking these against a series of so-called local α-error-levels:

The lowest *p*-value ($p_{[1]}$) is checked against α_F divided by the 'number of pairwise tests' ($\alpha_{[1]}$). If $p_{[1]} < \alpha_{[1]}$, then the second lowest *p*-value ($p_{[2]}$) is checked against α_F divided by 'number of pairwise tests' minus 1 ($\alpha_{[2]}$). If $p_{[2]} < \alpha_{[2]}$, then the attention turns to the third *p*-value, and so forth, until the last *p-value* ($p_{[n]}$) is checked against $\alpha_{[n]}$ (= α_F divided by 1 = α_F). As soon as any $p_{[x]} > \alpha_{[x]}$, the respective H_0 is accepted for this and all the following pairwise comparisons.

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[76] family-wise error rate = experiment-wise error rate (BORTZ, 1999): probability of wrongly rejecting global H_0 calculated across all simultaneous tests

[77] test-wise error rate (BORTZ, 1999): probability of wrongly rejecting global H_0 calculated for each of a number of simultaneous tests

[78] transl. by K. SCHUSTER

[79] Whenever the degree of dependence is not precisely known, however, adjustments of the α-error level will keep significance testing 'on the safe side'.

Example: At a significance level of **alpha**$_F$ = 0.05 and six pairwise comparisons, the six resulting *p*-values (in reverse order of magnitude, i.e., sorted from smallest to largest) are checked against the following sequentially adjusted α-error-values:

$\alpha_{[1]}$ equals 0.05* $^1/_6$ = 0.0083 → $p_{[1]}$ needs to be smaller than 0.0083
$\alpha_{[2]}$ equals 0.05* $^1/_5$ = 0.0100 → $p_{[2]} < 0.01$
$\alpha_{[3]}$ equals 0.05* $^1/_4$ = 0.0125 → $p_{[3]} < 0.0125$
$\alpha_{[4]}$ equals 0.05* $^1/_3$ = 0.0167 → $p_{[4]} < 0.0167$
$\alpha_{[5]}$ equals 0.05* $^1/_2$ = 0.0250 → $p_{[5]} < 0.025$
$\alpha_{[6]}$ equals 0.05* $^1/_1$ = 0.0500 → $p_{[6]} < 0.05$

During **focal-group** and **focal-animal analyses**, sequential **Bonferroni** adjustments were performed as a direct follow-up to a 'global test' (e.g., pair-wise Friedman-test following a significant result in a Friedman-test on several groups) to check for significances on the α_V-level of $p \leq 0.05$.

4.5 Comprehensive Schematic Overview of Steps Involved in Data Processing

The following three tables sum up the steps involved in data processing described in the sections above. This comprehensive schematic overview contrasts the different steps taken with respect to the examination of **focal groups** and **focal animals**. For the latter it further distinguishes between the 'examination level' of behavioural **elements** (accompanied by posture and heart rate) and behavioural **topography** (again, in conjunction with posture and heart rate). Information pertaining to focal groups (chapter 5.1) is presented in tab. 4-23[80], the respective details on focal-animal 'elementary' evaluations (chapter 5.2) are shown in tab. 4-21. The second table (tab. 4-22) provides a summary with respect to focal-animal 'topographical' evaluations (chapter 5.3).

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[80] for reader-friendly arrangement of two-page tables

Table 4-21: Overview of Steps involved in Data Processing – Focal-Animal Behaviour Elements, Posture, and Heart Rate (bpm). CR: Continuous Recording, ad lib.: Ad-Libitum Sampling; FA: focal animal; a, b, c: distance measure for conspecific disturbance, concentric circles around and in increasing distance from FA, with a = no nest in-between conspecific intruder and FA (directly at FA-nest), b = 1 nest in-between, and c = 2 nests in-between; IPIV-H: Interval-Performance Indicator Value for Human Visitation, IPIV-C: Interval-Performance Indicator Value for Conspecific Disturbance; ECG: electrocardiogram; appr.: approach, compl.: completely; s.a.: see above; correlations: Spearman's rho.

Parameter	**Categorisation**		**Primary Transcriptions**	
			Sampling	**Differentiation**
Penguin Behaviour s.l. (= behaviour s.s. and posture)	31 behaviour elements		CR (s-by-s)	within element categories: intensity (e.g., defensive/ offensive; small/ large head turns/ scans; compl. expressed/ intentional movements)
	2 postures		CR (s-by-s)	none
Penguin Heart Rate	ECG: heartbeats		beats per 20s (as counted)	none
Human Disturbance	4 visiting regimes	information on number of visitors (1 vs. 3); information on visitor conduct (loud and fast vs. silent and slow)	CR; s-by-s record of human visitation (written protocol, denoting start- and end-points in seconds), watch time aligned with video and logger	by visiting stage: initial approach to 15m distance from colony edge, time spent at 15m, approach to 5m, time spent at 5m, appr. to 3m, time spent at 3m, retreat
Conspecific Disturbance	moving at 3 distances from FA nest (a, b, c)	walking (moving at normal speed)	CR (s-by-s)	by nest distances (a, b, c)
		running		
	stationary at 3 distances from FA nest (a, b, c)	just standing/ lying (a, b, c)		
		manipulating FA nest, e.g., nest stone theft; interacting with FA (a)		by type of interaction
Predator/ Aircraft Disturbance	skua high, medium, low overflight; skua on ground; skua nest attack; bird shadow; aircraft noise		ad lib.	skua by height of overflight/ presence on ground; bird shadow: none aircraft: if possible, by type (helicopter, plane)

Secondary Transcriptions		**Analyses**	**Visualisation**
Sampling	**Differentiations**		
20s-intervals (rate and/or duration per interval)	same as during primary transcriptions	correlation of selected behaviour parameters with - conspecific disturbance - human visitation - heart rate	table
20s-intervals (rate and/or duration per interval)	none	not presented	not presented
20s-intervals (beats per minute, extrapolated)	none	correlation of heart rate with - conspecific disturbance - human visitation - selected behaviour parameters	table (s.a.)
20s-intervals (weighted sum of seconds of human presence)	**Interval-Performance Indicator Value for Human Visitation (IPIV-H):** weighted by distance from colony edge, visitor number and visitor conduct	s.a. (behaviour, heart rate)	table (s.a.)
20s-intervals (weighted sum of seconds of conspecifics present)	**Interval-Performance Indicator Value for Conspecific Disturbance (IPIV-C):** weighted by distance from FA, number of conspecifics, velocity of movement, type of interaction	s.a. (behaviour, heart rate)	table (s.a.)
ad lib.	skua by height of overflight/ presence on ground; bird shadow: none aircraft: if possible, by type (helicopter, plane)	not presented	not presented

Table 4-22: Overview of Steps involved in Data Processing – Focal-Animal Behavioural, Postural and Heart Rate Topopgraphy. CR: Continuous Recording, ad lib.: Ad-Libitum Sampling; FA: focal animal; a, b, c: distance measure for conspecific disturbance, concentric circles around and in increasing distance from FA, with a = no nest in-between conspecific intruder and FA (directly at FA-nest), b = 1 nest in-between, and c = 2 nests in-between; VS-PIV: Visiting-Stage Performance Indicator Value for Human Visitation, CMM: Conspecific Movement Measure; ECG: electrocardiogram; (R)HR: (resting) heart rate, SD: standard deviation; pre-dur-post: prior to, during, and after human visitation.

Parameter	Categorisation		Primary Transcriptions		Secondary Transcriptions	
			Sampling	Differentiation	Sampling	Differentiations
Penguin Behaviour s.l. (= behaviour s.s. and posture)	behaviour systems (composed of behaviour elements)	5 behaviour systems	CR (s-by-s)	within system categories: intensity (e.g., defensive/ offensive; moderate/ intense vigilance)	phases (time spent in a given behaviour system)	by contents (pure, impure, transitionary, types of interruption)
						by phase duration class
						none
	posture	2 postures	CR (s-by-s)	none	states (time spent in a given posture)	by state duration class
						none
Penguin Heart Rate	ECG: heartbeats	none	beats per 20s (as counted)	none	beats per 20s (as counted)	classified as undulating regularly/ increasing/ decreasing
						none
	deviations from resting heart rate (RHR ± 2SD)	below, within, above RHR ± 2SD			phases (time stretches of HR below, within, above RHR ± 2SD)	by phase duration class
						none
Human Disturbance	4 visiting regimes	information on number of visitors (1 vs. 3); information on visitor conduct (loud and fast vs. silent and slow)	CR; s-by-s record of human visitation (written protocol, denoting start- and end-points in seconds), watch time aligned with video and logger	by visiting stage: initial approach to 15m distance from colony edge, time spent at 15m, approach to 5m, time spent at 5m, appr. to 3m, time spent at 3m, retreat	nominally by visiting stage	**Visiting-Stage-Performance Indicator Value for Human Visitation (VS-PIV):** **N.b.:** differentiation by visiting stage only, no integration of number and conduct
Conspecific Disturbance	moving at three distances from FA nest (a, b, c)		CR (s-by-s)	by nest distances	for each distance: sum per 10s	**Conspecific Movement Measure** (CMM, per 2min-interval prior to disturbance)
						total conspecific movement (a, b, c); conspecific movement at the focal nest (a)
	stationary at closest distance from FA nest (a)			none	sum per 10s	conspecifc stationary presence at the focal nest
Predators/ Aircraft Disturbance	skua high, medium, low overflight; skua on ground; skua nest attack; bird shadow (skua, Southern giant petrel); aircraft noise		ad lib.	skua disturbance; aircraft noise	ad lib.	skua disturbance; aircraft noise

Analyses		Visualisation
Visual Appraisal	differences between periods = pre-dur-post	topography charts (individual sessions); tables (all groups; each group)
	differences between visiting stages	
	changes during increases/ decreases in total conspecific movement and conspecific movement at the focal nest	
	changes during increases/ decreases in conspecific stationary presence at the focal nest	
	changes during predator/ aircraft disturbance	
Quantitative Comparison	total time spent in each behaviour system pre-dur-post (all groups, each group, individual sessions); Friedman-test pre-dur-post (all groups)	boxplots; tables
Phase Number & Phase Time	differences between periods = pre-dur-post (all groups)	pie charts (total phase number & time); log diagrams (category phase number & time)
Visiting Regimes	for selected systems, ranked proportions calculated between periods = pre-dur-post; ranked magnitudes of difference between periods (each group)	tables depicting ranks
Visual Appraisal	see behaviour systems	see behaviour systems
Quantitative Comparison		
State Number & State Time		
Visiting Regimes		
Visual Appraisal	differences between periods = pre-dur-post	topography charts (individual sessions); tables (all groups; each group)
	differences between visiting stages)	
	changes during increases/ decreases in total conspecific movement and conspecific movement at the focal nest	
	changes during increases/ decreases in conspecific stationary presence at the focal nest	
	changes during predator/ aircraft disturbance	
Quant. Comparison: ‘visited’ vs. ‘baseline’ HR	changes between periods (‘visited’: pre-dur-post) and 10min-intervals ('baseline') with respect to 8 statistical parameters (all groups); Friedman-tests (all groups)	scatterplots (magnitude of difference from pre-visit/ 1st interval values); tables
Phase Number & Phase Time	differences between periods = pre-dur-post (all groups)	pie charts (total phase number & time); log diagrams (category phase number & time)
Visiting Regimes	ranked proportions calculated between periods = pre-dur-post; ranked magnitudes of difference between periods (each group)	tables depicting ranks
Visual Appraisal; Quant. Comparison; Phase Number & Time; Visiting Regimes	see behaviour/ heart rate	see behaviour/ heart rate
Visual Appraisal	change in CMM in successive 2min-intervals pre-visitation (all groups; each group)	topography charts (individual sessions); tables
	see behaviour/ heart rate	see behaviour/ heart rate
Visual Appraisal	see behaviour/ heart rate	see behaviour/ heart rate

Table 4-23: Overview of Steps involved in Data Processing – Focal Groups. AOS: All-Occurrences Sampling, CR: Continuous Recording, ISS: Instantaneous-Scan Sampling, OZS: One-Zero Sampling, ad lib.: Ad-Libitum Sampling; FG: focal group; PPIV-H: Point-Performance Indicator Value for Human Visitation, PPIV-C: Point-Performance Indicator Value for Conspecific Presence; row: a ‘string’ of focal-group nests in line with colony edge; 1st row: at colony edge, 2nd to 4th rows: in line with colony edge but separated from it by other rows of nests; 1st to nth per row: first to last (focal-group nests in a row were denoted from left to right); PUI-G: ‘Penguin Unit’-Index per focal group, PUI-R: ‘Penguin Unit’-Index per row; pre-dur-post: prior to, during, and after human visitation; n.a.: not applicable; (partial) correlations: Spearman’s rho.

Parameter	Categorisation		Primary Transcriptions		Secondary Transcriptions		Analyses	Visualisation
			Sampling	Differentiation	Sampling	Differentiations		
Penguin Behaviour s.l. (= behaviour s.s. and posture)	3 behaviour aspects	6 behaviour states	ISS (30s point sampling)	by row (1st to 4th)	ISS (30s point sampling)	**Penguin-Unit-Index, PUI-R:** per row (1st, 2nd, 3rd, 4th)	differences between periods = pre-dur-post per row	pie charts; tables: values for each period = pre-dur-post, magnitudes of difference between periods pre → dur, dur → post
						Penguin-Unit-Index, PUI-G: total group (sum of 1st to 4th)	differences between periods = pre-dur-post for all rows together (total)	
		1 behaviour event	AOS (30s interval sampling)	by row (1st to 4th) and nest (1st to n-th per row)	OZS (yes/ no per nest and 30s interval)	**Penguin-Unit-Index, PUI-R:** per row (1st, 2nd, 3rd, 4th)	differences between periods = pre-dur-post per row	
						Penguin-Unit-Index, PUI-G: total group (sum of 1st to 4th)	differences between periods = pre-dur-post for all rows together (total)	
		2 posture states	ISS (30s point sampling)	by row (1st to 4th)	ISS (30s point sampling)	**Penguin-Unit-Index, PUI-R:** per row (1st, 2nd, 3rd, 4th)	differences between periods = pre-dur-post per row	
						Penguin-Unit-Index, PUI-G: total group (sum of 1st to 4th)	differences between periods = pre-dur-post for all rows together (total)	
Penguin Heart Rate	none obtained for FG		n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Human Disturbance	4 visiting regimes	information on number of visitors (1 vs. 3); information on visitor conduct (loud and fast vs. silent and slow)	CR; s-by-s record of human visitation (written protocol, denoting start- and end-points in seconds), watch time aligned with video and logger	by visiting stage: initial approach to 15m distance from colony edge, time spent at 15m, approach to 5m, time spent at 5m, appr. to 3m, time spent at 3m, retreat	ISS (30s point sampling)	**Point-Performance Indicator Value for Human Visitation (PPIV-H):** integration of distance, visitor number and visitor conduct	correlations: conspecific presence during visitation with human visitation (PPIV-C and PPIV-H)	tables
							partial correlations: human visitation with selected behavioural parameters and posture (conspecific presence partialled out)	
Conspecific Disturbance	conspecific presence	no distinction between stationary and moving conspecifics	ISS (30s point sampling)	by location relative to focal group: outside colony, edge, between 1st and 2nd row, …, between 4th and 5th row	ISS (30s point sampling)	**Point-Performance Indicator Value for Conspecific Presence (PPIV-C):** total sum of conspecifics, as no row differences detected for focal-group behaviour	correlations: conspecific presence pre and post with selected behavioural parameters and posture	tables
							partial correlations: conspecific presence during visitation with selected behavioural parameters and posture (human visitation partialled out)	
Predator/ Aircraft Disturbance	skua high, medium, low overflight; skua on ground; skua nest attack; bird shadow (skua, Southern giant petrel); aircraft noise		ad lib.	skua by height of overflight/ presence on ground; bird shadow: none aircraft: if possible (helicopter, plane)	used for elimination of data points clearly affected by predator/ aircraft disturbance		n.a.	n.a.

5 Results

The results ‘super-chapter’ comprises three parts presenting results on different types of evaluation which may be considered chapters in their own right, viz.,

1. Results on **focal-group** behaviour **aspects** (behaviour states, behaviour event, posture; chapter 5.1)
2. A very brief summary on results pertaining to **focal-animal** behaviour **elements** and heart rate (published elsewhere; chapter 5.2)
3. Results on **focal-animal** behavioural, postural and heart rate **topography** (chapter 5.3) in which topography is examined with respect to three different key questions (How many?, How much?, In what way?)

To improve intra-thesis orientation and provide the reader with an overview before delving into diverse details, **interim summaries** have been placed **at the beginning** rather than the end of sections, while **chapter summaries** are found **at the end**.

As regards chapter 5.3, the same structure was opted for on the level of each key question (i.e., interim summaries before detailed results, key question summary at the end), and answers obtained for all three key questions are drawn together in a final chapter summary.

5.1 Responses of Groups of Penguins to Disturbance: Behaviour and Posture

The study of group responses (behaviour, posture) was undertaken to examine whether human visitation might cause overall shifts in behavioural reaction patterns.

Focal-Group Sampling (see chapter 4.2.2) was considered the appropriate method to compare occurrence and prevalence of different behaviours/ postures in the absence of human visitors to their occurrence and prevalence observed during four different visiting regimes. Rather than tracing individual birds, the whole group is therefore focused upon in this section (group changes in behaviour/ posture).

For focal groups, 30 sessions (from 4 groups) in the course of which human visitation had taken place constituted the database (tab. 5.1-1). Numbers of incubating birds were complemented by a fluctuating number of **conspecifics** ‘on the move’.

Table 5.1-1: Database Used for Focal-Group Sampling. B, C, X, Y: focal groups; S&S: silent and slow; L&F: loud and fast; 1 P: single visitor; 3 P: three visitors; B_1, C_1/ B_2, C_2: datasets obtained prior to and after a switch in visiting regimes (at groups B and C, after approx. two-thirds of the observation period).

Dataset	Total Sessions per Dataset	1 P, S&S	1 P, L&F	3 P, S&S	3 P, L&F
sessions B_1	8	0	8	0	0
sessions B_2	3	3	0	0	0
sessions C_1	6	6	0	0	0
sessions C_2	3	0	3	0	0
sessions X	5	0	0	5	0
sessions Y	5	0	0	0	5
total sessions	30	9	11	5	5

5.1.1 Methodological Prelude

Recapitulation: Groups B and C had been subjected to a **switch in visiting regime**; the subsets are presented as datasets **B**$_1$ (1 P, L&F), **C**$_1$ (1 P, S&S) and **B**$_2$ (1 P, S&S), and **C**$_2$ (1 P, L&F), respectively. Visiting regimes for groups **X** (3 P, S&S) and **Y** (3 P, L&F) had not been changed, resulting in a **total of six datasets** from four focal groups (tab. 5.1-1)

Behaviour and posture were transcribed in four nest **rows** of increasing distance to the source of human disturbance (fig. 5.1-1).

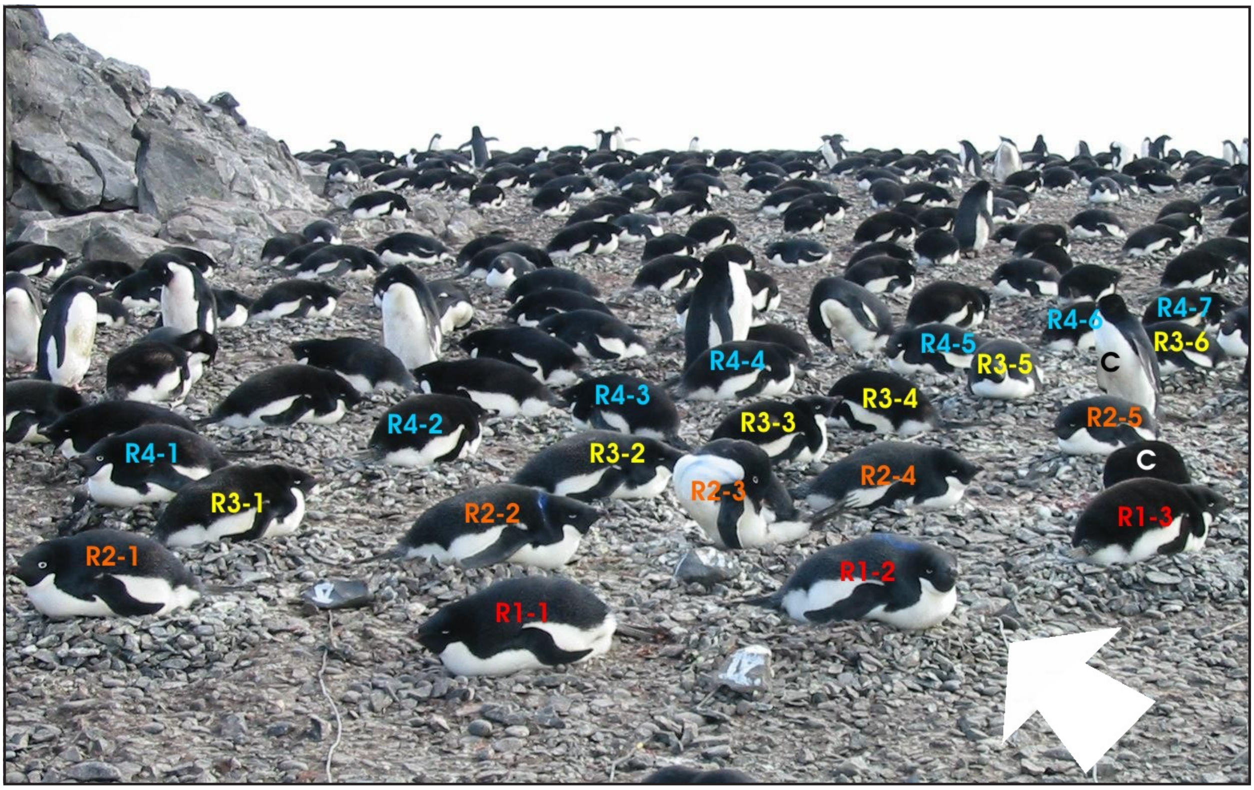

Figure 5.1-1: Recapitulation: Assignment of rows. The screenshot taken at the beginning of each data transcription served to assign nests to rows of increasing distance from the source of human disturbance (R1 - R4). Conspecifics (C) currently not engaged in incubation were also identified in the screenshot. In each row, nesting penguins were marked from left to right (here: R1-1, R1-2, etc.). The white arrow indicates the direction from which the human visitor(s) approached. © K.Schuster 2001

During **primary** transcriptions (from tape onto paper), two time sampling methods (chapter 4.2.2.1, tab. 4-3) had been combined for maximum efficiency: Instantaneous-Scan Sampling (ISS) had assigned the incubating birds' behaviours to six behaviour states (alert, agonistic, flippers-up, preen, manipulate, or rest&Co) and two postural states (prone or up) every 30 s, while All-Occurrences Sampling[1] (AOS) had served to count the number of headshakes performed by each bird (behaviour event) during the 30 s-interval preceding the scan sampling point.

5.1.1.1 Secondary Transcription of Behaviour/ Posture

For **secondary** transcriptions, data from the (hard-copy) transcription sheets were entered into Excel spreadsheets (Microsoft, 1997/ 2003; see exemplary matrix in appendix 5.1-1). Instantaneous-Scan Sampling data (behaviour states and posture) were matricised the way they had been originally transcribed (i.e. numbers of incubating penguins per row assigned to each category).

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[1] Given that headshake reactions are of short duration (event, rather than state), their occurrence would have been inaccurately represented by Instantaneous-Scan Sampling.

All-Occurrences Sampling data (occurrence of headshakes) were **modified** as follows:

For each individual it was noted whether they had performed **at least one** headshake per interval[2]. Although this effectively reduced the information gathered to the level generally obtained by One-Zero Sampling, this method was considered to yield more appropriate results, as it directly reflected the number of penguins reacting, rather than representing a mixture of 'more penguins' and 'the same penguin more often' – and thus permitted OZS-results to be compared to those obtained by Instantaneous-Scan Sampling.

While All-Occurrences Sampling is highly useful when examining individual differences among the penguins, at this stage, row/ group reactions were in the focus of the analyses.

5.1.1.1.1 Penguin-Unit-Index (PUI)

Rendering group reactions comparable[3] across sessions, as well as between different rows and datasets, required a proportionalisation procedure. For this reason, a **'penguin unit'-index** (PUI) was devised. This index corrected not only for differences in the number of penguins per dataset or row, but also for differences in number of sampling units (points or intervals).

For **each period** (before, during, after human visitation), the number of penguins that could be unequivocally assigned to a given behaviour/ posture category per sampling point or interval was summed up over all sampling points or intervals included in the period, and divided by the sum of birds observed at all sampling points or intervals included in the period[4].

'Penguin unit'-index per row (= R1, R2, R3, R4) – PUI-R

e.g. for R1, 'alert'

$$\frac{\sum \text{alert per period } (\text{R1,1} + \text{R1,2} + \ldots + \text{R1, n})}{\sum \text{sampling points per period } (\text{R1,1} + \text{R1,2} + \ldots + \text{R1, n})}$$

'Penguin unit'-index for entire focal group (= R_{tot} = R1+R2+R3+R4) – PUI-G

e.g. for focal group, 'alert'

$$\frac{\sum \text{alert per period } (\text{R1,1} + \text{R1,2} + \ldots + \text{R4, n})}{\sum \text{sampling points per period } (\text{R1,1} + \text{R1,2} + \ldots + \text{R4, n})}$$

The proportionalisation procedure described above results in values ranging from 0.00 to 1.00, with larger values indicating a greater proportion of penguins assigned to the respective category.

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[2] For each penguin, the exact number of headshakes was noted in the **primary matrices**, but occurrence (yes/ no) of headshakes within a given interval was entered into the **secondary matrices** and used for evaluations. Thus, sums per interval give information on the number of penguins performing at least one headshake within a given interval, NOT on the number of headshakes.

[3] Due to slight day-to-day differences in camera angle and zoom, the total number of nests varied across sessions.

[4] N.b.: In the following equations, the Σ-sign is merely used as shorthand for 'sum of'.

5.1.1.2 Secondary Transcription of Disturbance

5.1.1.2.1 Human Visitation – Point Performance Indicator Value for Human Disturbance (PPIV-H)

For secondary transcriptions, the components of human visitation identified previously (distance, conduct, number) were categorised and coded as shown in table 5.1-2.

Total human disturbance at a given sampling point was then calculated as the sum of applicable code-values. The resulting sum at a given sampling point constituted the **Point Performance Indicator Value** for Human Disturbance (PPIV-H).

Table 5.1-2: Categorisation of Disturbance during Human Visitation (Focal-Group Analyses). At each sampling point, the sum of applicable code-values constitutes the Point Performance Indicator Value for Human Disturbance (PPIV-H).

Visitor Distance	**Code**
no visitation	1
approach to 15m/ at 15m	3
approach to 5m/ at 5m	4
approach to 3m/ at 3m	5
retreat	2
Visitor Conduct (Type)	**Code**
no visitation	1
silent and slow (S&S)	2
loud and fast (L&F)	4
Visitor Number	**Code**
no visitation	1
one visitor (1 P)	2
three visitors (3 P)	4

Example: For loud and fast conduct (code value = 4) of one visitor (= 2) at 5 m distance from the penguins (= 4), **PPIV-H** would total 10 at any sampling point for which these conditions applied.

If a transition between distances (e.g., approach from 15 m to 5 m) had taken place within the preceding sampling interval, the proportion of time the visitor(s) had spent at each distance was taken into account by assigning the point to the distance the visitor(s) had held during the greater proportion of the interval. PPIV-H was entered into Excel and SPSS matrices for correlations with focal-group behaviour/ posture.

5.1.1.2.2 Conspecific 'Disturbance' – Point Performance Indicator Value for Conspecific Presence (PPIV-C)

Categorisation of conspecific total 'disturbance' considered the number of conspecifics present in six predetermined areas from 'outside colony' to 'between fourth and fifth row' of nests. While separate transcription had served well as a guard against losing track of numbers, only the sum of conspecifics was used in analyses: As the exact location of each conspecific will be close to some birds in the focal group and more distant to others, their total number, rather than their specific position, was considered to represent the potential impact on groups.

Total **conspecific presence** was thus used as an **approximation of total 'disturbance'** at a given point and constituted the **Point Performance Indicator Value** for Conspecific Presence (PPIV-C). PPIV-C was entered into Excel and SPSS matrices for correlations with focal-group behaviour/ posture.

5.1.1.2.3 Predator/ Aircraft Disturbance

Ad libitum sampling notations in the ‘remarks’-column of primary transcriptions were entered into a corresponding column in the Excel matrices. While systematic evaluation was impossible due to rare and ‘erratic’ occurrences, these notes helped to gauge whether changes in the focal group’s behaviour were likely to result from sources of disturbance other than human or conspecific (chapter 4.3.4.7, q.v.).

5.1.1.3 Presentation of Results

5.1.1.3.1 Absolute and Magnitudinal Results

Whenever there are distinct between-row or between-dataset differences prior to human visitation (pre-), however, it is misleading to simply compare **absolute** results during or after human visitation across rows or datasets, because absolute penguin-unit-values make no distinction between ‘a leap and a crawl’.

Example: The scenario ‘few birds were standing prior to human visitation’ (e.g., absolute penguin-unit-value$_{pre}$: 0.02), and then ‘many more got up during visitation’ (resulting in, e.g., penguin-unit-value$_{dur}$: 0.13)’ differs strongly from that of ‘many birds were standing right from the start’ (e.g., penguin-unit-value$_{pre}$: 0.11), and then ‘a few more got up during human visitation’ (equally resulting in, e.g., penguin-unit-value$_{dur}$: 0.13)’, but the difference between the scenarios is not reflected in the absolute penguin-unit-values.

In those cases, differences were assessed by comparing the **magnitude of the change**. This was done by subtracting the absolute penguin-unit-values of the respective period from those of the previous period (i.e., ‘during visit’ minus ‘pre-visit’, ‘post-visit’ minus ‘during visit’) so that **positive values** indicated an **increase** relative to the previous period, while **negative values** pointed to a **decrease**.

5.1.1.3.2 Friedman-Test

Friedman-test was performed to examine whether differences in the behaviour of penguins nesting in different rows of increasing distance from the human disturbance were statistically significant. In case of significant results, pair-wise Friedman-tests (and sequential Bonferroni adjustments, q.v.) were calculated to detect between which rows the significant difference existed.

5.1.1.3.3 Colour Codes

The colour codes used to facilitate visual discrimination of significance levels (tab. 5.1-3) as well as r^2-values (transformed correlation coefficients; tab. 5.1-4) have been introduced in chapter 4.4. They are repeated here.

Table 5.1-3 (= Table 4-20): Colour Codes for Significance Levels for α_F = Overall Significance.

4	$0.0001 \leq p < 0.001$	very highly significant
3	$0.001 \leq p < 0.01$	highly significant
2	$0.01 \leq p < 0.05$	significant
1	$0.05 \leq p < 0.1$	tendentially significant

Table 5.1-4 (= Table 4-19): Colour Codes for and Informal Interpretation of r^2-Values, Modified Following SPRINTHALL (1987).

5	**$0.810 \leq r^2 < 1.000$**	**very high** correlation, very dependable relationship (not in these datasets)
4	$0.490 \leq r^2 < 0.810$	**high** correlation, marked relationship
3	$0.160 \leq r^2 < 0.490$	**moderate** correlation, substantial relationship
2	$0.100 \leq r^2 < 0.160$	**low** correlation, definite but small relationship
1	$0.001 \leq r^2 < 0.100$	**slight** correlation, almost negligible relationship

5.1.1.3.4 Order of Presentation

The first section on ***period differences on the group level*** demonstrates the extent to which parameters differed before, during, and after human visitation.

Results on ***row differences*** in the following section are used to examine a possible influence of distance from the disturbance stimulus. Results of ***Friedman-tests*** serve to gauge the statistical significance of differences found.

In the last section, results on the relation between ***intensity of response and type of disturbance*** are presented for selected parameters of each behaviour aspect.

Results on ***correlations*** of focal-group responses to conspecific presence before and after human visitation are followed by those on ***partial correlations*** between focal-group responses to conspecific presence during visitation, and to human visitation itself.

Within chapter 5.1, the following **order of presentation** has been adhered to: Results in each section are presented first for behaviour states ('alert', 'agonistic', etc.), then for the behaviour event ('occurrence of headshakes'), and finally for postures ('prone', 'up').

In each of these 'packages', results on ***predominance*** of categories (i.e., which category was shown by most penguins most of the time) are presented first, followed by an overview on differences ***between periods*** and/or ***rows***. Subsequently, more detailed results on differences ***between groups*** (before human visitation), and differences ***between regimes*** (during and after visitation) are mentioned. The 'package' closes with a description of effects of the ***switch in visiting regime*** – or their absence (groups B and C only).

5.1.2 Group Differences

Dividing each session into three periods, viz. time before the visit (pre-), time during the visit (during-, s.t. abbreviated to 'dur') and time after the visit (post-), **pie charts** are presented to gain an overview with respect to differences in the distribution of behaviours within these periods. Three aspects of behaviour are presented: Behaviour states ('alert', 'agonistic', etc.), one behaviour event ('occurrence of headshakes_yes' or '_none'), and postures ('prone' or 'up').

For each group, **pie charts** show the mean of all sessions that had been conducted under the same visiting regime[5] (see tab. 5.1-1). In the **tabulated overviews**, mean values for each dataset have been summarised per parameter; these are complemented by minimum, median, and maximum values calculated across all datasets.

For each of the three aspects, results are presented to the following **questions addressed** on the **group level**:

- Did the groups vary with respect to the predominant behaviour category/ categories?
- Did the groups vary with respect to between-period differences (before to during, during to after, before to after visitation)?
- To what extent did the groups differ prior to visitation?
- Did between-regime differences (during and after visitation) exhibit a specific pattern (i.e., a gradient consistent with severity of the visiting regime)?

5.1.2.1 Section Summary

The ***predominant*** categories in all datasets and periods were represented by the categories ‘alert’ and/or ‘rest&Co’ for the aspect ‘behaviour states’, ‘headshakes_none’ (aspect ‘behaviour event’), and ‘prone’ (aspect ‘posture’).

Between-period differences were found in all datasets and for all three aspects examined: Median index-values **during** human visitation (during-visit) differed from those **prior to** visitation (pre-visit), and returned to approximately pre-visitation level **after** the visits (post-visit). **During** human visitation, the increase in index-levels was most prominent in the category ‘alert’ (behaviour states; increase: +0.14). It was complemented by a decrease in the category ‘rest&Co’ (behaviour states: decrease: -0.13). To a much lesser degree index-values also increased in the categories ‘headshakes_yes’ (behaviour event; increase: +0.04) and ‘up’ (posture; increase: +0.02).

Between-group differences **prior to** visitation were mostly small for the categories ‘headshakes_yes’ (aspect ‘behaviour event’) and ‘up’ (aspect ‘posture’). Concerning the aspect ‘behaviour states’, two categories, viz., ‘alert’ and ‘rest&Co’, exhibited substantial between-group differences prior to visitation so that between-period differences were assessed by looking at the magnitude of the decrease/ increase of index-values.

Between-regime differences **during** and **after** human visitation were mostly slight in the categories ‘headshakes_yes’ (aspect ‘behaviour event’) and ‘up’ (aspect ‘posture’). With respect to the categories ‘alert’ and ‘rest&Co’ (aspect ‘behaviour states’), between-regime differences could be arranged along the following **gradient of decreasing response** for four of the six datasets[6] : Initial exposure to ‘one visitor, loud and fast’ (dataset B$_1$), exposure to ‘three visitors, loud and fast’ (group Y), exposure to ‘three visitors, silent and slow’ (group X), and initial exposure to ‘one visitor, silent and slow’ (dataset C$_1$).

Following, results are presented in detail.

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[5] With respect to groups B and C (2000), the visiting regime had been switched after approximately $^2/_3$ of the fieldwork period (B$_1$: 1 P, L&F → B$_2$: 1 P, S&S; C$_1$: 1 P, S&S → C$_2$: 1 P, L&F).

[6] Dataset B$_2$ (1 P, S&S) and dataset C$_2$ (1 P, L&F) did not readily fit into this gradient.

5.1.2.2 Behaviour States

For the following passage, the reader is referred to figure 5.1-2 and table 5.1-5.

Predominant index-values in **all periods** and datasets were calculated for vigilance behaviour (‘alert’, with medians between 0.51 and 0.67) and/or for the category ‘rest&Co’ (with medians between 0.25 and 0.39). With two exceptions (‘post-switch’ datasets[7]), between-period increase in the one category was complemented by a decrease in the other and vice versa. The remaining categories were noted far less frequently (all medians below 0.10)[8], and generally, differences were neither readily discernible between periods, nor between datasets. Reasons for this are suggested in chapter 6.1.3.1.

For the categories ‘alert’ and ‘rest&Co’, ***between-period differences*** were distinct in all datasets and visiting regimes, with vigilance behaviour increasing **during** visits, while the behaviours subsumed in the category ‘rest&Co’ decreased. **After** human visitation, the respective index-values more or less resembled those calculated for pre-visit behaviour.

There were distinct ***between-group differences*** **prior to human visitation** (pre-), particularly with respect to ‘alert’ (range: 0.40 to 0.68) and ‘rest&Co’ (range: 0.19 to 0.50)[9] . Therefore, behavioural reactions **during** and **after** the visits were assessed by looking at the magnitude of the within-group change rather than at absolute penguin-unit-values (see section 5.1.1.3.1). **During** visits, the median increase in vigilance (‘alert’) amounted to +0.14 (range: +0.05 to +0.28) penguin units, while index-values of the category ‘rest&Co’ exhibited a median decrease of -0.13 (range: -0.26 to -0.5).

Between-regime differences in magnitude of response were evident **during** human visitation: Birds initially subjected to the regime 1 P, S&S (dataset C_1) exhibited the smallest change in behaviours (‘alert’: increase +0.05; ‘rest&Co’: decrease -0.05), while those initially subjected to the regime 1 P; L&F (dataset B_1) showed the largest (‘alert’: increase +0.28; ‘rest&Co’: decrease -0.26). For groups X (3 P, S&S) and Y (3 P, L&F), changes in index-values were considerably greater (tab. 5.1-5) than those for dataset C_1 (1 P, S&S), but did not reach those attained by dataset B_1 (1 P, L&F).

In the groups that were subjected to a ***switch in visiting regime*** (with B_2: 1 P, S&S; and C_2: 1 P; L&F), changes in index-values after the switch were comparatively small for both ‘alert’ and ‘rest&Co’. This apparent ‘lack of response’ in the two otherwise predominant categories occurred irrespective of visiting regime or direction of the switch. During this time, the category ‘manip’ (comprising nest manipulation and egg or chick manipulation) achieved a greater prominence in some periods (B_2: pre-visitation; C_2: during visitation), but not in others. No distinct changes were found in the remaining categories (viz., ‘agonistic’, ‘preen’, ‘flippers-up’; tab. 5.1-5).

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[7] viz., B_2 (1 P, S&S) pre-visit; and C_2 (1 P, L&F) during-visit; for which the increase/ decrease occurred in the category ‘manip’

[8] In the category ‘manip’, medians ranged from 0.06 (during-visit) to 0.08 (pre-visit); in the other categories, they fell between 0.00 and 0.03.

[9] Additionally, in the category ‘manip’, the index-value for B_2 prior to visitation represented an outlier (0.13; all others 0.06 to 0.08).

Table 5.1-5: Overview – Descriptive Statistics Concerning Distribution of Different Categories of Three Behaviour Aspects of Focal-Group Behaviour Examined. Mean values (all sessions) are shown for each dataset; these are complemented by minimum (min.), median (med.), and maximum (max.) values calculated across all datasets. Rtot: sum across all four rows; Alert: vigilance behaviour, Agon: agonistics, Fl-up: flippers up, Manip: manipulate (egg and nest manipulation), Preen: preening; Rest&Co: resting/ sleeping and small comfort behaviours (yawning, 'non-committal' movements), Headshakes_yes: headshakes occurred, Up: sitting/ standing posture; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; L&F: loud and fast, S&S: silent and slow; 1 P: one visitor, 3 P: three visitors; pre: prior to visitation, dur: during visitation, post: after visitation, dur-pre: difference between pre- and during-visitation, post-dur: difference between during- and post-visitation.

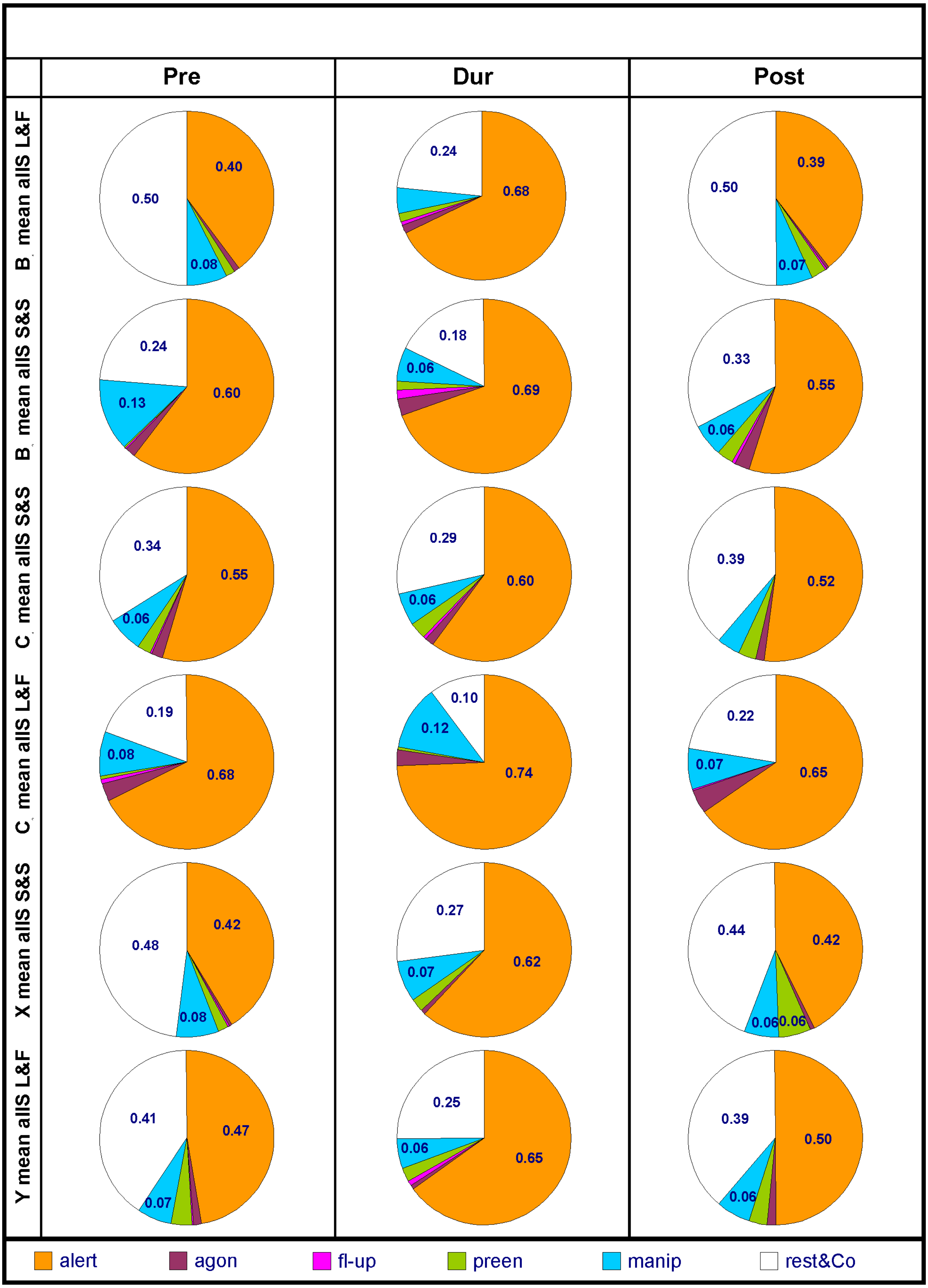
	Alert					**Preen**				
group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
B_1_1P_L&F	0.40	0.28	0.68	-0.29	0.39	0.02	0.00	0.02	0.01	0.03
B_2_1P_S&S	0.60	0.09	0.69	-0.14	0.55	0.00	0.02	0.02	0.01	0.03
C_1_1P_S&S	0.55	0.05	0.60	-0.08	0.52	0.03	0.00	0.03	0.00	0.03
C_2_1P_L&F	0.68	0.06	0.74	-0.09	0.65	0.01	0.00	0.01	-0.01	0.00
X_3P_S&S	0.42	0.20	0.62	-0.20	0.42	0.02	0.00	0.02	0.04	0.06
Y_3P_L&F	0.47	0.18	0.65	-0.15	0.50	0.04	-0.02	0.02	0.01	0.03
min	0.40	0.05	0.60	-0.29	0.39	0.00	-0.02	0.01	-0.01	0.00
med	**0.51**	**0.14**	**0.67**	**-0.15**	**0.51**	**0.02**	**0.00**	**0.02**	**0.01**	**0.03**
max	0.68	0.28	0.74	-0.08	0.65	0.04	0.02	0.03	0.04	0.06

	Agon					**Manip**				
group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
B_1_1P_L&F	0.01	0.00	0.01	0.00	0.01	0.08	-0.03	0.05	0.02	0.07
B_2_1P_S&S	0.02	0.01	0.03	0.00	0.03	0.13	-0.07	0.06	0.00	0.06
C_1_1P_S&S	0.02	0.00	0.02	0.00	0.02	0.06	0.00	0.06	-0.02	0.04
C_2_1P_L&F	0.03	0.00	0.03	0.01	0.04	0.08	0.04	0.12	-0.05	0.07
X_3P_S&S	0.00	0.01	0.01	0.00	0.01	0.08	-0.01	0.07	-0.01	0.06
Y_3P_L&F	0.01	0.00	0.01	0.01	0.02	0.07	-0.01	0.06	0.02	0.08
min	0.00	0.00	0.01	0.00	0.01	0.06	-0.07	0.05	-0.05	0.04
med	**0.02**	**0.00**	**0.02**	**0.00**	**0.02**	**0.08**	**-0.01**	**0.06**	**-0.01**	**0.07**
max	0.03	0.01	0.03	0.01	0.04	0.13	0.04	0.12	0.02	0.08

	Fl-up					**Rest&Co**				
group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
B_1_1P_L&F	0.00	0.01	0.01	-0.01	0.00	0.50	-0.26	0.24	0.26	0.50
B_2_1P_S&S	0.00	0.01	0.01	-0.01	0.00	0.24	-0.06	0.18	0.15	0.33
C_1_1P_S&S	0.00	0.01	0.01	-0.01	0.00	0.34	-0.05	0.29	0.10	0.39
C_2_1P_L&F	0.01	-0.01	0.00	0.00	0.00	0.19	-0.09	0.10	0.12	0.22
X_3P_S&S	0.00	0.00	0.00	0.00	0.00	0.48	-0.21	0.27	0.17	0.44
Y_3P_L&F	0.00	0.01	0.01	-0.01	0.00	0.41	-0.16	0.25	0.14	0.39
min	0.00	-0.01	0.00	-0.01	0.00	0.19	-0.26	0.10	0.10	0.22
med	**0.00**	**0.01**	**0.01**	**-0.01**	**0.00**	**0.38**	**-0.13**	**0.25**	**0.15**	**0.39**
max	0.01	0.01	0.01	0.00	0.00	0.50	-0.05	0.29	0.26	0.50

	Headshakes_yes					**Up**				
group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
B_1_1P_L&F	0.05	0.04	0.09	-0.02	0.07	0.06	0.02	0.08	-0.02	0.06
B_2_1P_S&S	0.16	-0.01	0.15	-0.07	0.08	0.10	0.03	0.13	-0.03	0.10
C_1_1P_S&S	0.07	0.02	0.09	-0.02	0.07	0.07	0.02	0.09	-0.02	0.07
C_2_1P_L&F	0.14	0.02	0.16	-0.01	0.15	0.13	0.03	0.16	-0.04	0.12
X_3P_S&S	0.07	0.05	0.12	-0.05	0.07	0.09	0.03	0.12	-0.02	0.10
Y_3P_L&F	0.06	0.02	0.08	-0.02	0.06	0.09	0.00	0.09	-0.01	0.08
min	0.05	-0.01	0.08	-0.07	0.06	0.06	0.00	0.08	-0.04	0.06
med	**0.07**	**0.02**	**0.11**	**-0.02**	**0.07**	**0.09**	**0.03**	**0.11**	**-0.02**	**0.09**
max	0.16	0.05	0.16	-0.01	0.15	0.13	0.03	0.16	-0.01	0.12

Figure 5.1-2: Mean Distribution of Six Behaviour States before, during, and after Human Visitation. allS: all sessions per dataset; L&F: loud and fast, S&S: silent and slow; 1 P: one visitor, 3 P: three visitors; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; B_1: 1 P, L&F; B_2: 1 P, S&S; C_1: 1 P, S&S; C_2: 1 P, L&F; X: 3 P, S&S; Y: 3 P, L&F; Rtot: sum across all four rows; alert: vigilance behaviour; agon: agonistics, fl-up: flippers up, manip: manipulate (egg and nest manipulation), preen: preening; rest&Co: resting/ sleeping and small comfort behaviours (yawning, 'non-committal' movements).



5.1.2.3 Behaviour Event

For the following passage, the reader is referred to figure 5.1-3 and table 5.1-5.

Predominant index-values in **all periods** and datasets were calculated for the category ‘headshakes_none’[10] (medians between 0.89 and 0.93).

Overall, ***period-differences*** were small: **Before** human visitation (pre-), index-values for ‘headshakes_yes’ ranged from 0.05 to 0.16 (median: 0.07). With the exception of group B after the switch in visiting regime (from dataset B_1: 1 P, L&F to dataset B_2: 1 P, S&S), the category ‘headshakes_yes’ increased **during** human visitation (range during-visit: 0.08 to 0.16; median: 0.11). **After** the visits (post-), it decreased in all datasets, and (excepting dataset B_2 = group B after the switch in visiting regime) index-values more or less resembled those calculated for pre-visitation (range: 0.06 to 0.15; median: 0.07).

Between-group differences **prior to visitation** as well as ***between-regime differences*** **during** and **after** human visitation were mostly small, but singled out datasets B_2 and C_2 (s.b.).

Groups B and C exhibited considerably higher index-values for ‘headshakes_yes’ after the ***switch in visiting regime*** (comparing dataset B_1 to dataset B_2 and dataset C_1 to dataset C_2). In spite of the groups’ being subjected to different visiting regimes, the respective index-values obtained for datasets B_2 (1 P, S&S) and C_2 (1 P, L&F) were not distinctly different (comparing dataset B_2 to dataset C_2). Furthermore, the direction of the switch ($B_1 \rightarrow B_2$: from ‘loud and fast’ to ‘silent and slow’; $C_1 \rightarrow C_2$: the other way round) did not appear to have had any influence. The fact that higher values than prior to the switch were observed in all periods (i.e., not only during visitation), suggests the difference to be (mainly) due to changes in the colony resulting from a more advanced stage in the breeding cycle (i.e., beginning of hatching time).

5.1.2.4 Posture

For the following passage, the reader is referred to figure 5.1-4 and table 5.1-5.

Predominant index-values in **all periods** and datasets were calculated for the category ‘prone’[11] (medians between 0.89 and 0.91).

Between-period differences in penguin-unit-index calculated for the category ‘up’, were slight.

Between-group differences **before** human visitation were likewise small; and there were no distinct ***between-regime differences*** either **during** or **after** human visitation: For the category ‘up’, the median index-value **before** human visitation (pre-) was 0.09 (range: 0.06 to 0.13), **during** human visitation (during-) it was marginally higher (0.11; range: 0.08 to 0.16), and **after** human visitation (post-) it decreased by about the same magnitude to a median of 0.09 (range: 0.06 to 0.12).

With respect to groups B and C, the category ‘up’ became more prominent in all periods after the ***switch in visiting regime***. For datasets B_2 (1 P, S&S) and C_2 (1 P, L&F), there was no distinct difference between visiting regimes; nor did the direction of the switch ($B_1 \rightarrow B_2$: from ‘loud and fast’ to ‘silent and slow’; $C_1 \rightarrow C_2$: the other way round) appear to have had any influence.

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[10] N.b.: headshakes_none = 1 - headshakes_yes (cf. tab. 5.1-5)

[11] N.b.: posture ‘prone’ = 1 – posture ‘up’ (cf. tab. 5.1-5)

Figure 5.1-3: Mean Distribution of Occurrence and Absence of Headshake Events before, during, and after Human Visitation. allS: all sessions per dataset; L&F: loud and fast, S&S: silent and slow; 1 P: one visitor, 3 P: three visitors; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; B_1: 1 P, L&F; B_2: 1 P, S&S; C_1: 1 P, S&S; C_2: 1 P, L&F; X: 3 P, S&S; Y: 3 P, L&F; Rtot: sum across all four rows; yes/ none: headshakes occurred/ did not occur.

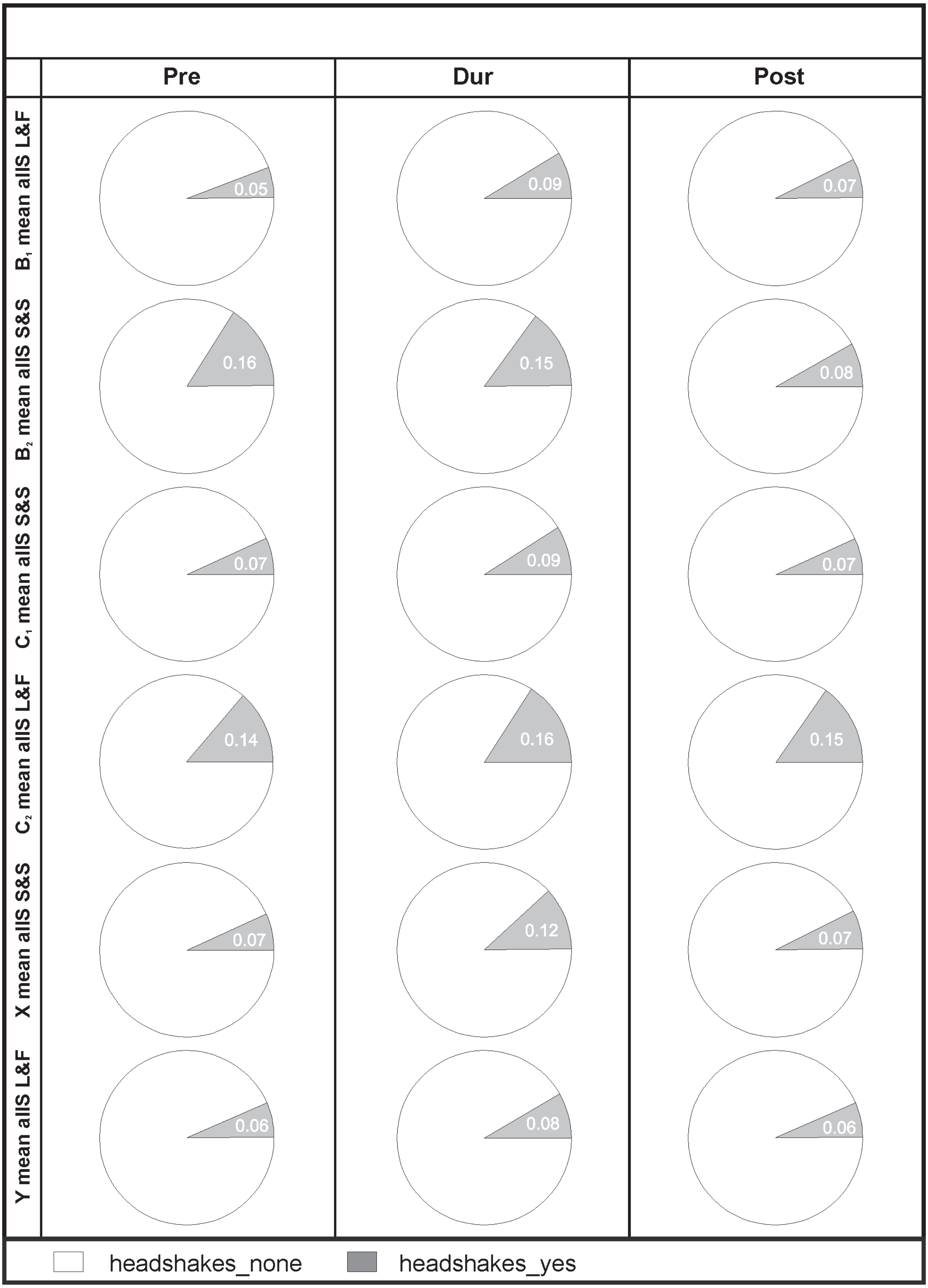
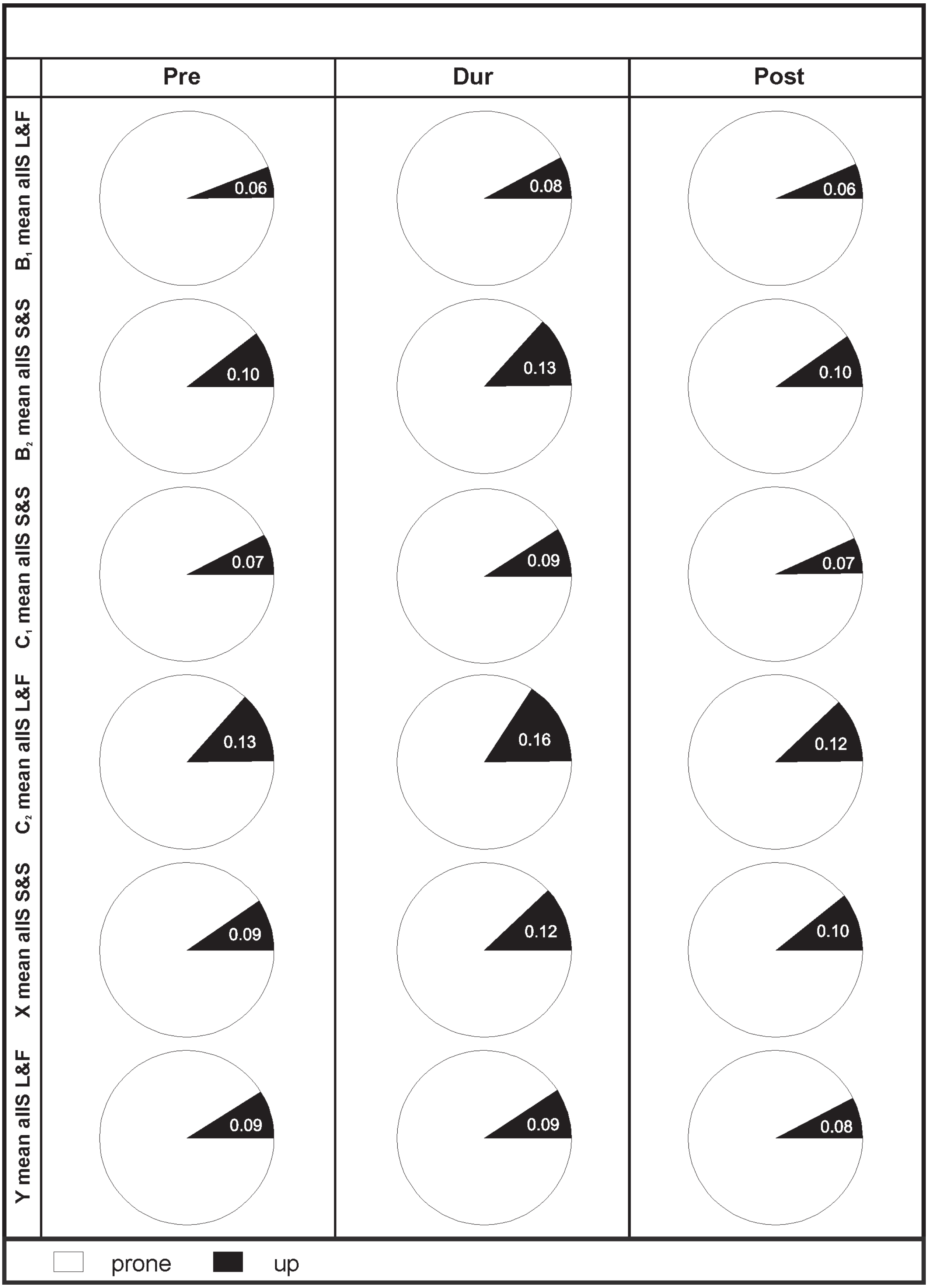


Figure 5.1-4: Mean Distribution of Two Postures before, during, and after Human Visitation. allS: all sessions per dataset; L&F: loud and fast, S&S: silent and slow; 1 P: one visitor, 3 P: three visitors; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; B_1: 1 P, L&F; B_2: 1 P, S&S; C_1: 1 P, S&S; C_2: 1 P, L&F; X: 3 P, S&S; Y: 3 P, L&F; Rtot: sum across all four rows; prone: lying, up: sitting/ standing.



5.1.3 Row Differences

Having found differences between the three periods (viz., before and after human visitation vs. during human visitation) in all datasets examined, it was considered necessary to check whether penguins nesting in an increasing distance from the human visitor contributed equally to these findings. For this, data obtained on the respective rows (R1-R4) were evaluated separately.

For each of the three behaviour aspects (six behaviour states, one behaviour event, and two postures) reactions to human visitation of penguins nesting in four different rows of increasing distance from the source of disturbance are presented. For each of the six datasets[12] (i.e., B_1, B_2, C_1, C_2, X, Y), pie charts were created for the mean[13] of a given row for all sessions that had been conducted under the same visiting regime (see tab. 5.1-6) To facilitate comparisons, pie charts on all rows pooled are presented above (R_{tot}; i.e., these are identical with those of the previous section) the pie charts for each of the rows (R1, R2, R3, and R4).

For each of the three aspects, results are presented to the following **questions addressed** on the **row level**:

- Did the predominant category/ categories in each row reflect that/ those found for the whole group?
- Did between-period differences for each row reflect those found for the whole group?
- To what extent did the rows differ in a given period (viz., before, during, after visitation)?
- Did between-row differences exhibit a specific pattern (e.g., a gradient consistent with distance from the human visitor(s)?

5.1.3.1 Section Summary

In all datasets and periods, the ***predominant*** category/ categories (i.e., ‘alert’ and/or ‘rest&Co’, ‘headshakes_none’, and ‘prone’) in each row reflected that/ those found for the whole group.

Between-period differences for each row frequently did not reflect those found for the whole group. Greater values (than those calculated for R_{tot}) were most often obtained for R1 and/or R2 in the categories ‘alert’, ‘rest&Co’ and ‘headshakes_yes’, and for R1 and/or R4 in the category ‘up’ (for statistical significance, see below).

Before human visitation, *between-row differences* existed for all three aspects, but did not exhibit any clear pattern (i.e., no gradients). **After** human visitation, differences between the rows existed for all three aspects, but with the exception of the category ‘alert’, in which R1 values were the highest among all rows in five datasets out of six, there was no clear pattern (i.e., no gradients) discernable.

During visitation, R1 index-values of the categories ‘alert’, ‘rest&Co’, and ‘headshakes_yes’ were often greater (i.e., higher for ‘alert’ and ‘headshakes_yes’; lower for ‘rest&Co’) than those of the other rows. Furthermore, concerning the categories ‘alert’ and ‘rest&Co’, a **gradient in magnitude of response** was found in groups X (3 P, S&S) and Y (3 P, L&F).

No pattern was detected with respect to the category ‘up’.

As with the exception of two cases, pairwise **Friedman-tests** did not find significant differences between the rows, results presented in section 5.1.4 are therefore based on focal groups with no

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[12] Recapitulation: The terms group and dataset refer to the same ‘body of birds’ in groups X and Y (no switch in visiting regime); with respect to groups B and C, the switch in visiting regimes resulted in two datasets (pre-switch, post-switch) for each group.

[13] The **arithmetic mean** was used whenever data of the same dataset were averaged (across sessions or rows).

distinctions made between the rows. The tendency to stronger responses found in R1 birds should, however, be kept in mind.

Following, results are presented in detail.

5.1.3.2 Behaviour States

For this passage, the reader is referred to figures 5.1-5 – 5.1-10 and table 5,1-6. To facilitate between-row comparisons, table 5.1-6 provides the statistical overview only with respect to the categories presented in more detail in the text; the complete overview is found in appendix 5.1-2.

Predominant index-values in _all rows_, **all periods** (and all datasets) were calculated for the categories ‘alert’ (range of median index-values: 0.48 to 0.77; see tab. 5.1-6) and/or ‘rest&Co’ (range of median index-values: 0.11 to 42).

The category ‘manip’ (comprising nest/ egg manipulation) attained greater index-values than the category ‘rest&Co’ three times (B_2, 1 P, S&S pre-visit: R3 = 0.16; C_2, 1 P, L&F during visit: R3 = 0.15 and R4 = 0.12), but did not come close to those calculated for the category ‘alert’. The remaining categories were more or less negligible in each row (range of median index-values: 0.00 to 0.05), again reflecting results obtained for pooled rows (R_{tot}, see previous section).

For the categories ‘alert’ and ‘rest&Co’, ***between-period differences*** (i.e., increases/ decreases from one period to the next) were generally greater for R1 and/or R2, and smaller for R3 and/or R4 (as compared to those calculated for all rows together, see tab. 5.1-6).

Before human visitation, *between-row differences* were frequent for the categories ‘alert’ and ‘rest&Co’, but did not exhibit a clear pattern in any of the datasets.

During human visitation, the highest index-values for the category ‘alert’ were calculated for the first row (R1) in five out of the six datasets (excepting dataset C_2); in each case, this was complemented by the lowest index-values for the category ‘rest&Co’ (again excepting dataset C_2). Moreover, with respect to groups X (3 P, S&S) and Y (3 P, L&F), there was a gradual decrease (‘alert’: R1 > R2 > R3 > R4) resp. increase (‘rest&Co’: R1 < R2 < R3 < R4) in index-values, although for group Y, index-values in R3 and R4 were reversed (i.e. R4 exhibited slightly higher values for ‘alert’ and lower values for ‘rest&Co’ than R3).

After the visits, R1 index-values for ‘alert’ were the highest among all rows in five datasets out of six (excepting dataset B_2), but the pattern was not as distinct as during visitation. As for the category ‘rest&Co’, there was no clear pattern discernable.

After the ***switch in visiting regime***, index-values for ‘alert’ calculated for dataset B_2 (1 P, S&S) were distinctly higher (as compared to dataset B_1) **before** and **after** the visits for R2-R4 but only slightly higher before and after the visits for R1. **During** visits, they remained approximately the same for all rows. This way, between-period differences were all but wiped out in R2-R4, but remained distinct in R1 (see tab. 5.1-6: alert-B_2 vs. alert-B_1). Index-values for ‘rest&Co’ were (considerably) lower (again, as compared to dataset B_1), both before and after the visits for all rows. They remained (approximately) the same during visits, resulting in much lower between-period differences than had been calculated prior to the switch in visiting regime.

As for dataset C_2 (1 P, L&F), index-values for ‘alert’ calculated after the switch in visiting regime were higher, and index-values for ‘rest&Co’ were lower than before the switch (i.e., as compared to dataset C_1) in _all rows_ and **all periods**.

No consistent differences were found with respect to the remaining categories (appendix 5.1-2).

Table 5.1-6: Overview – Descriptive Statistics Concerning Distribution of Four Parameters of Focal-Group Behaviour Examined for Each of Four Rows. Mean values (all sessions) are shown for each dataset; these are complemented by minimum (min.), median (med.), and maximum (max.) values calculated across all datasets. R1: first row, R2: second row, R3: third row, R4: fourth row; alert: vigilance behaviour; rest&Co: resting/ sleeping and small comfort behaviours (yawning, 'non-committal' movements), headshakes_yes: headshakes occurred, up: sitting/ standing posture; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; L&F: loud and fast, S&S: silent and slow; 1 P: one visitor, 3 P: three visitors; pre: prior to visitation, dur: during visitation, post: after visitation, dur-pre: difference between pre- and during-visitation, post-dur: difference between during- and post-visitation. **N.b.:** Only values for parameters presented in detail in the text are provided in this table, the complete table is found in appendix 5.1-2.

		R1					R2				
Alert	group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
	B_1 L&F	0.44	0.37	0.81	-0.36	0.45	0.33	0.33	0.66	-0.32	0.34
	B_2 S&S	0.55	0.26	0.81	-0.31	0.50	0.60	0.09	0.69	-0.17	0.52
	C_1 S&S	0.57	0.08	0.65	-0.04	0.61	0.51	0.09	0.60	-0.12	0.48
	C_2 L&F	0.75	-0.02	0.73	-0.03	0.70	0.56	0.12	0.68	-0.06	0.62
	X S&S	0.50	0.20	0.70	-0.20	0.50	0.34	0.30	0.64	-0.27	0.37
	Y L&F	0.53	0.30	0.83	-0.26	0.57	0.47	0.23	0.70	-0.16	0.54
	min	0.44	-0.02	0.65	-0.36	0.45	0.33	0.09	0.60	-0.32	0.34
	med	**0.54**	**0.23**	**0.77**	**-0.23**	**0.54**	**0.49**	**0.18**	**0.67**	**-0.17**	**0.50**
	max	0.75	0.37	0.83	-0.03	0.70	0.60	0.33	0.70	-0.06	0.62
Rest&Co	group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
	B_1 L&F	0.49	-0.39	0.10	0.37	0.47	0.57	-0.29	0.28	0.28	0.56
	B_2 S&S	0.21	-0.11	0.10	0.28	0.38	0.24	-0.04	0.20	0.17	0.37
	C_1 S&S	0.30	-0.06	0.24	0.07	0.31	0.43	-0.18	0.25	0.17	0.42
	C_2 L&F	0.19	-0.08	0.11	0.09	0.20	0.25	-0.09	0.16	0.11	0.27
	X S&S	0.42	-0.25	0.17	0.25	0.42	0.50	-0.23	0.27	0.17	0.44
	Y L&F	0.36	-0.29	0.07	0.22	0.29	0.39	-0.20	0.19	0.14	0.33
	min	0.19	-0.39	0.07	0.07	0.20	0.24	-0.29	0.16	0.11	0.27
	med	**0.33**	**-0.18**	**0.11**	**0.24**	**0.35**	**0.41**	**-0.19**	**0.23**	**0.17**	**0.40**
	max	0.49	-0.06	0.24	0.37	0.47	0.57	-0.04	0.28	0.28	0.56
Headshakes_yes	group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
	B_1 L&F	0.05	0.06	0.11	-0.04	0.07	0.04	0.05	0.09	-0.05	0.04
	B_2 S&S	0.10	0.02	0.12	-0.05	0.07	0.20	-0.06	0.14	-0.09	0.05
	C_1 S&S	0.11	0.04	0.15	-0.04	0.11	0.05	0.06	0.11	-0.04	0.07
	C_2 L&F	0.12	0.19	0.31	-0.15	0.16	0.16	-0.04	0.12	-0.02	0.10
	X S&S	0.07	0.08	0.15	-0.09	0.06	0.08	0.05	0.13	-0.04	0.09
	Y L&F	0.06	0.04	0.10	-0.02	0.08	0.07	0.03	0.10	-0.03	0.07
	min	0.05	0.02	0.10	-0.15	0.06	0.04	-0.06	0.09	-0.09	0.04
	med	**0.09**	**0.05**	**0.14**	**-0.05**	**0.08**	**0.08**	**0.04**	**0.12**	**-0.04**	**0.07**
	max	0.12	0.19	0.31	-0.02	0.16	0.20	0.06	0.14	-0.02	0.10
Up	group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
	B_1 L&F	0.07	0.06	0.13	-0.05	0.08	0.06	-0.01	0.05	-0.01	0.04
	B_2 S&S	0.05	0.04	0.09	-0.01	0.08	0.07	0.00	0.07	-0.04	0.03
	C_1 S&S	0.08	0.04	0.12	-0.06	0.06	0.04	0.07	0.11	-0.05	0.06
	C_2 L&F	0.02	0.12	0.14	-0.10	0.04	0.14	-0.08	0.06	0.02	0.08
	X S&S	0.08	0.07	0.15	-0.06	0.09	0.11	0.00	0.11	0.02	0.13
	Y L&F	0.07	0.02	0.09	0.00	0.09	0.11	0.00	0.11	-0.03	0.08
	min	0.02	0.02	0.09	-0.10	0.04	0.04	-0.08	0.05	-0.05	0.03
	med	**0.07**	**0.05**	**0.13**	**-0.06**	**0.08**	**0.09**	**0.00**	**0.09**	**-0.02**	**0.07**
	max	0.08	0.12	0.15	0.00	0.09	0.14	0.07	0.11	0.02	0.13

		R3					R4				
Alert	group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
	B_1 L&F	0.37	0.28	0.65	-0.25	0.40	0.42	0.17	0.59	-0.21	0.38
	B_2 S&S	0.67	-0.04	0.63	-0.13	0.50	0.65	0.02	0.67	0.01	0.68
	C_1 S&S	0.56	0.07	0.63	-0.06	0.57	0.54	-0.01	0.53	-0.06	0.47
	C_2 L&F	0.74	0.04	0.78	-0.13	0.65	0.70	0.07	0.77	-0.12	0.65
	X S&S	0.48	0.12	0.60	-0.15	0.45	0.37	0.16	0.53	-0.11	0.42
	Y L&F	0.40	0.11	0.51	-0.11	0.40	0.49	0.08	0.57	-0.09	0.48
	min	0.37	-0.04	0.51	-0.25	0.40	0.37	-0.01	0.53	-0.21	0.38
	med	**0.52**	**0.09**	**0.63**	**-0.13**	**0.48**	**0.52**	**0.08**	**0.58**	**-0.10**	**0.48**
	max	0.74	0.28	0.78	-0.06	0.65	0.70	0.17	0.77	0.01	0.68
Rest&Co	group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
	B_1 L&F	0.48	-0.24	0.24	0.24	0.48	0.49	-0.18	0.31	0.18	0.49
	B_2 S&S	0.14	0.08	0.22	0.13	0.35	0.25	-0.09	0.16	0.05	0.21
	C_1 S&S	0.28	0.00	0.28	0.06	0.34	0.35	0.00	0.35	0.07	0.42
	C_2 L&F	0.13	-0.08	0.05	0.11	0.16	0.18	-0.09	0.09	0.14	0.23
	X S&S	0.43	-0.15	0.28	0.16	0.44	0.58	-0.20	0.38	0.04	0.42
	Y L&F	0.48	-0.09	0.39	0.11	0.50	0.40	-0.06	0.34	0.10	0.44
	min	0.13	-0.24	0.05	0.06	0.16	0.18	-0.20	0.09	0.04	0.21
	med	**0.36**	**-0.09**	**0.26**	**0.12**	**0.40**	**0.38**	**-0.09**	**0.33**	**0.09**	**0.42**
	max	0.48	0.08	0.39	0.24	0.50	0.58	0.00	0.38	0.18	0.49
Headshakes_yes	group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
	B_1 L&F	0.07	0.00	0.07	0.00	0.07	0.06	0.02	0.08	0.01	0.09
	B_2 S&S	0.19	-0.04	0.15	-0.02	0.13	0.14	0.02	0.16	-0.08	0.08
	C_1 S&S	0.08	0.00	0.08	-0.02	0.06	0.05	0.01	0.06	-0.01	0.05
	C_2 L&F	0.14	0.00	0.14	0.05	0.19	0.12	0.03	0.15	0.01	0.16
	X S&S	0.06	0.02	0.08	-0.01	0.07	0.06	0.06	0.12	-0.05	0.07
	Y L&F	0.07	0.00	0.07	-0.01	0.06	0.05	0.01	0.06	-0.01	0.05
	min	0.06	-0.04	0.07	-0.02	0.06	0.05	0.01	0.06	-0.08	0.05
	med	**0.08**	**0.00**	**0.08**	**-0.01**	**0.07**	**0.06**	**0.02**	**0.10**	**-0.01**	**0.08**
	max	0.19	0.02	0.15	0.05	0.19	0.14	0.06	0.16	0.01	0.16
Up	group	pre	dur-pre	dur	post-dur	post	pre	dur-pre	dur	post-dur	post
	B_1 L&F	0.07	0.00	0.07	-0.02	0.05	0.04	0.02	0.06	0.01	0.07
	B_2 S&S	0.14	-0.02	0.12	0.01	0.13	0.12	0.09	0.21	-0.08	0.13
	C_1 S&S	0.10	-0.04	0.06	0.00	0.06	0.07	0.01	0.08	0.01	0.09
	C_2 L&F	0.12	0.05	0.17	-0.01	0.16	0.18	0.04	0.22	-0.08	0.14
	X S&S	0.12	0.00	0.12	-0.02	0.10	0.06	0.04	0.10	-0.01	0.09
	Y L&F	0.09	-0.02	0.07	0.01	0.08	0.07	0.03	0.10	-0.05	0.05
	min	0.07	-0.04	0.06	-0.02	0.05	0.04	0.01	0.06	-0.08	0.05
	med	**0.11**	**-0.01**	**0.10**	**-0.01**	**0.09**	**0.07**	**0.04**	**0.10**	**-0.03**	**0.09**
	max	0.14	0.05	0.17	0.01	0.16	0.18	0.09	0.22	0.01	0.14

Figure 5.1-5: Dataset B_1 (1 P, L&F): Mean Distribution of Six Behaviour States before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; L&F: loud and fast; 1 P: one visitor; B_1: dataset prior to switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; alert: vigilance behaviour, agon: agonistics, fl-up: flippers up, manip: manipulate (egg and nest manipulation), preen: preening, rest&Co: resting/ sleeping and small comfort behaviours (yawning, 'non-committal' movements).

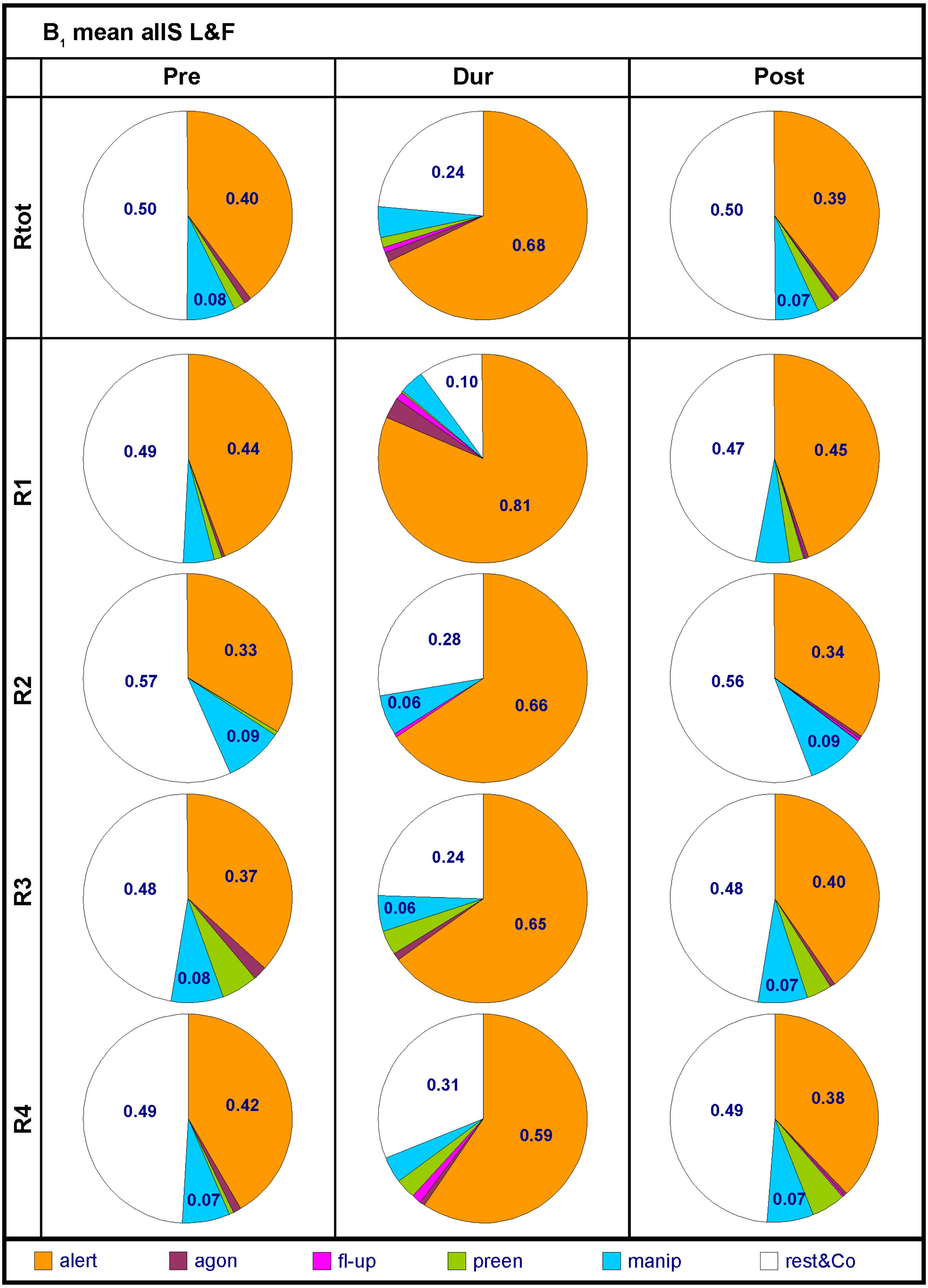


Figure 5.1-6: Dataset B_2 (1 P, S&S): Mean Distribution of Six Behaviour States before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; S&S: silent and slow; 1 P: one visitor; B_2: dataset after switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; alert: vigilance behaviour, agon: agonistics, fl-up: flippers up, manip: manipulate (egg and nest manipulation), preen: preening, rest&Co: resting/ sleeping and small comfort behaviours (yawning, ‘non-committal’ movements).

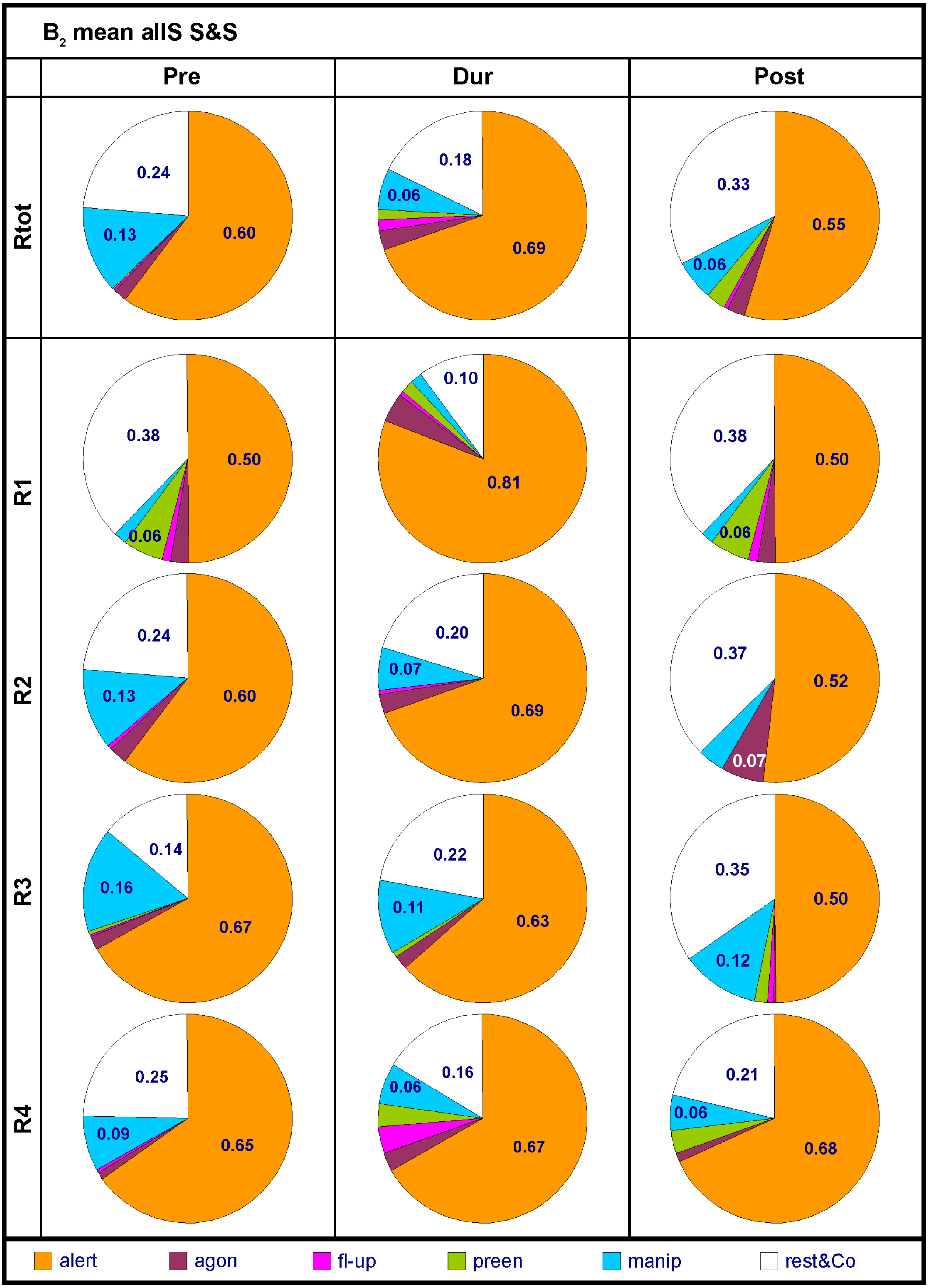


Figure 5.1-7: Dataset C_1 (1 P, S&S): Mean Distribution of Six Behaviour States before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; S&S: silent and slow; 1 P: one visitor; C_1: dataset prior to switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; alert: vigilance behaviour, agon: agonistics, fl-up: flippers up, manip: manipulate (egg and nest manipulation), preen: preening, rest&Co: resting/ sleeping and small comfort behaviours (yawning, 'non-committal' movements).

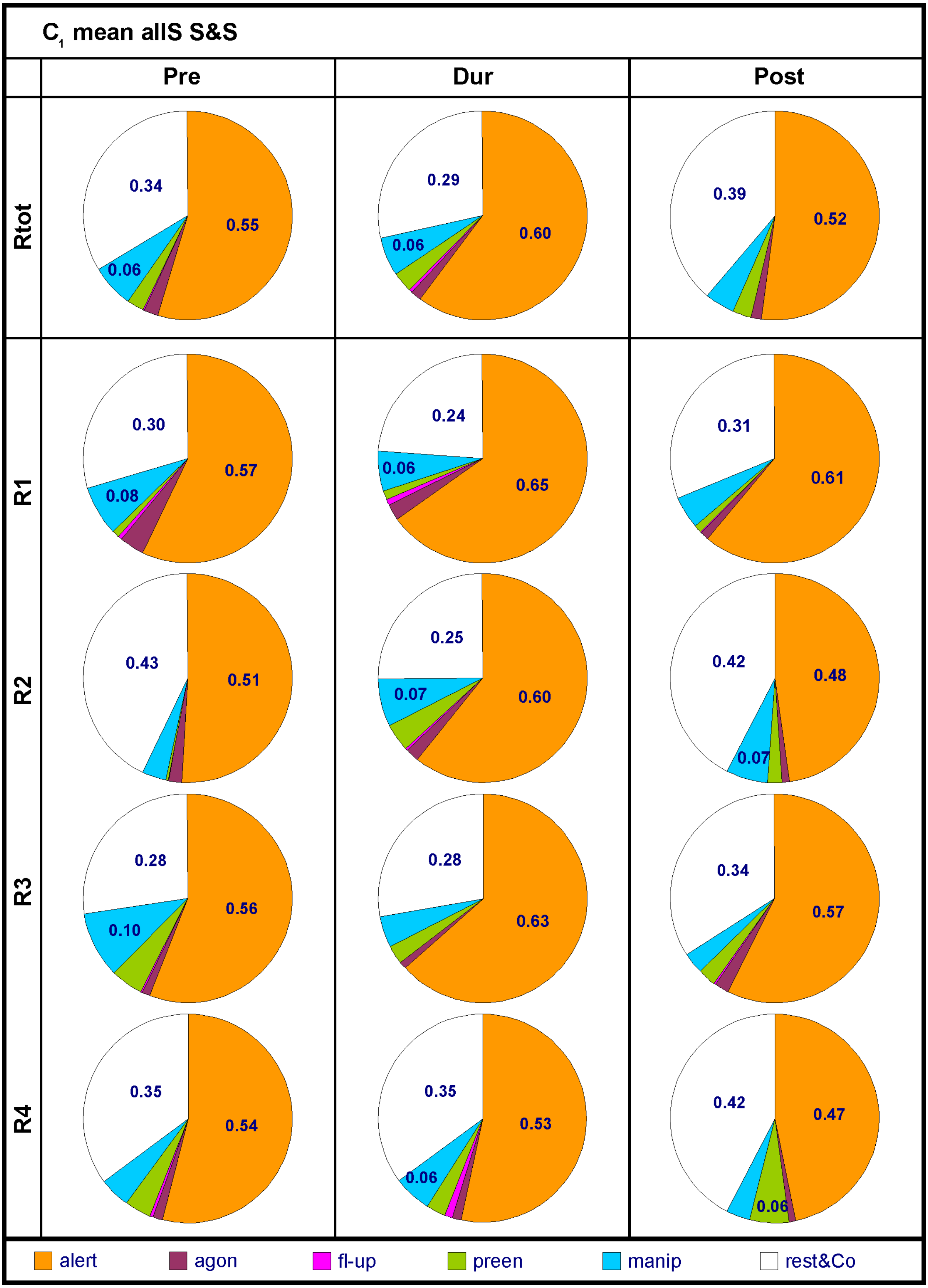


Figure 5.1-8: Dataset C_2 (1 P, L&F): Mean Distribution of Six Behaviour States before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; L&F: loud and fast; 1 P: one visitor; C_2: dataset after switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; alert: vigilance behaviour, agon: agonistics, fl-up: flippers up, manip: manipulate (egg and nest manipulation), preen: preening, rest&Co: resting/ sleeping and small comfort behaviours (yawning, 'non-committal' movements).

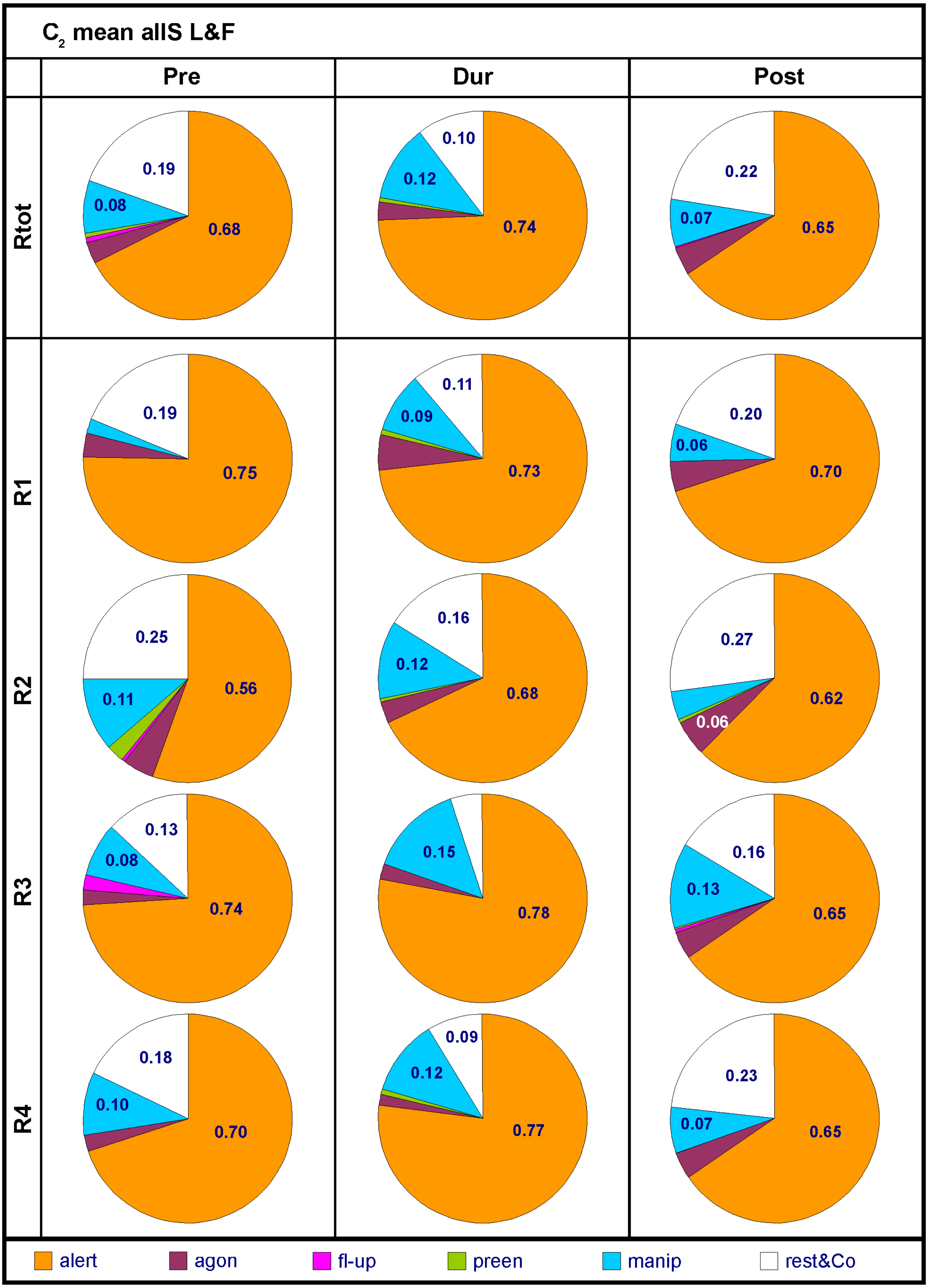


Figure 5.1-9: Group X (3 P, S&S): Mean Distribution of Six Behaviour States before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; S&S: silent and slow; 3 P: three visitors; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; alert: vigilance behaviour, agon: agonistics, fl-up: flippers up, manip: manipulate (egg and nest manipulation), preen: preening, rest&Co: resting/ sleeping and small comfort behaviours (yawning, ‘non-committal’ movements).

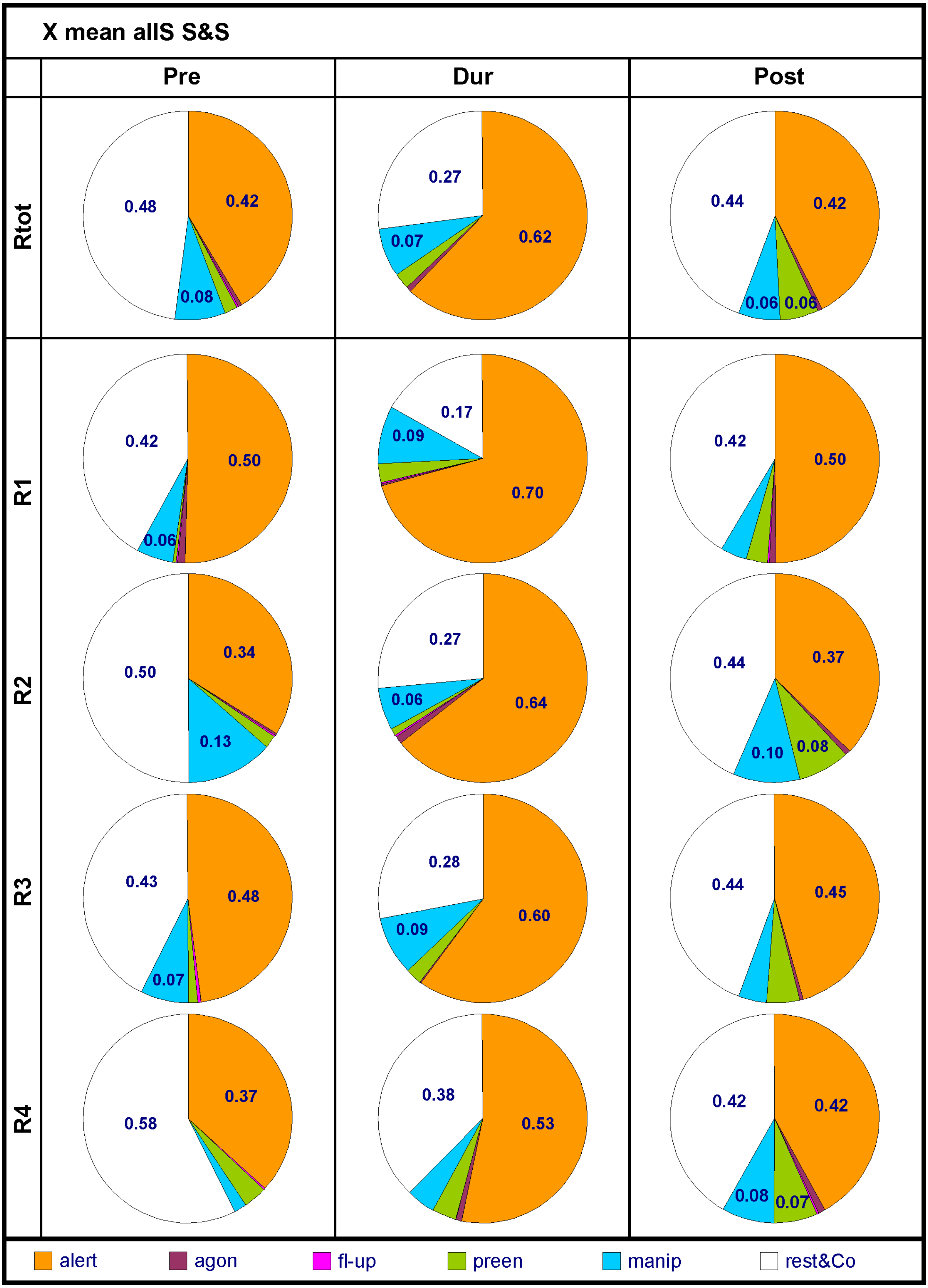
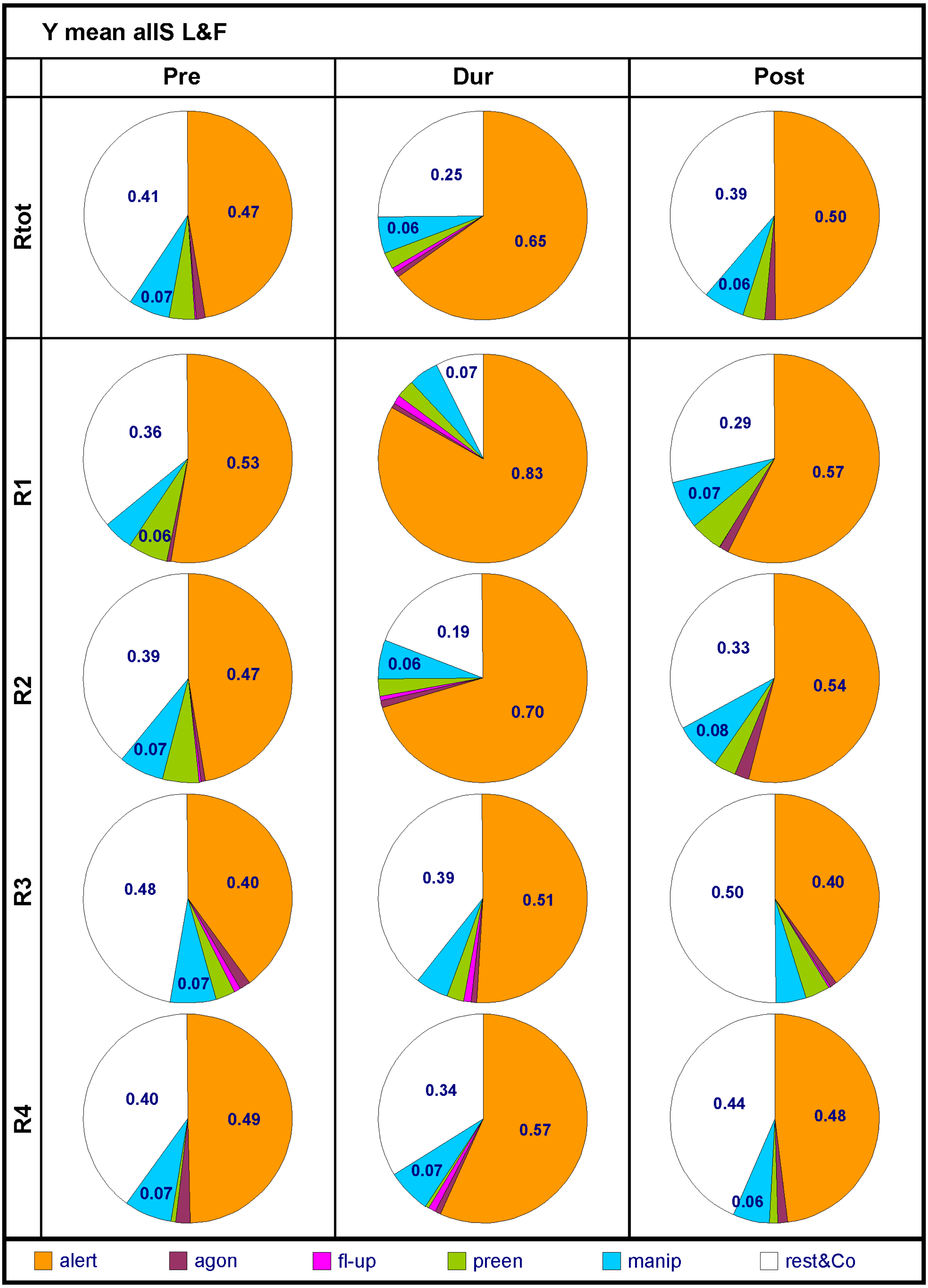


Figure 5.1-10: Group Y (3 P, L&F): Mean Distribution of Six Behaviour States before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; L&F: loud and fast; 3 P: three visitors; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; alert: vigilance behaviour, agon: agonistics, fl-up: flippers up, manip: manipulate (egg and nest manipulation), preen: preening, rest&Co: resting/ sleeping and small comfort behaviours (yawning, ‘non-committal’ movements).



5.1.3.3 Behaviour Event

For this passage, the reader is referred to figures 5.1-11 – 5.1-16 and table 5.1-6.

Predominant index-values in *all rows*, **all periods** (and all datasets) were calculated for the category ‘headshakes_none’ (figs. 5.1-11 – 5.1-16; range of median index-values: 0.86 to 0.94; for headshakes_yes values = 1 – headshakes_none, see tab. 5.1-6).

As for the category ‘headshakes_yes’, ***between-period differences*** (i.e., increases/ decreases from one period to the next) were more variable on the row level than those calculated for the entire datasets (R_{tot}: rows 1, 2, 3, 4) for only two of the six datasets: Within-group ranges were similar to the between-group range[14] in four datasets, considerably higher in one dataset (C_2: 1 P, L&F) and lower for group Y (3 P, L&F). Concerning R1, changes in index-values in the category ‘headshakes_yes’ were nearly always[15] above average (R_{tot}) and showed greater differences than those calculated for the following rows in five of the six datasets.

Prior to human visitation, *between-row differences* were slight and did not exhibit any consistent pattern in any of the datasets (figs. 5.1-11 – 5.1-16).

During human visitation, *between-row differences* frequently ‘separated’ R1 from those of the other rows (figs. 5.1-11 – 5.1-16): R1 index-values were greater in four of the six datasets and smaller in one dataset (B_2: 1 P, S&S). In the remaining one (3 P, L&F, group Y), the gap was located between R2 and R3, as index-values were identical for R1 and R2 (0.10; 0.10) and higher than those calculated for R3 and R4 (0.07; 0.06). **After** human visitation, there was no clear pattern discernable in any of the regimes.

With respect to dataset B_2, the generally higher (R_{tot}) index-values calculated for the category ‘headshakes_yes’ after the ***switch in visiting regime*** were not reflected in all rows and periods. Index-values for R1 were below average (R_{tot}) throughout; and showed the least increase (compared to index-values for dataset B_1) both **before** and **during** visits. R2 and R3 contributed most to the general increase in index-values (R_{tot}) before visits, R3 and R4 during visits; and R3 was the only row to exhibit distinctly higher index-values **after** visits (again, as compared to index-values for dataset B_1).

As for dataset C_2, the overall picture was different. Compared to dataset C_1, index-values were distinctly higher in almost all rows and periods[16]. While index-values for R2-R4 did not greatly change between periods, the R1 index-value **during** visits (0.31; increase pre- → during-: +0.19; decrease during- → post-: -0.15) was the highest recorded in all datasets and regimes (fig. 5.1-11).

---

[14] for differences between pre-visit and during-visit: -0.01 to 0.05; for differences between during-visit and post-visit: -0.07 to -0.01

[15] exception: dataset B_2 (1 P, S&S)

[16] only negligibly higher in $R1_{\text{pre and post}}$, $R2_{\text{dur and post}}$

Figure 5.1-11: Dataset B_1 (1 P, L&F): Mean Distribution of Occurrence and Absence of Headshake Events before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; L&F: loud and fast; 1 P: one visitor; B_1: dataset prior to switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; yes/ none: headshakes occurred/ did not occur.

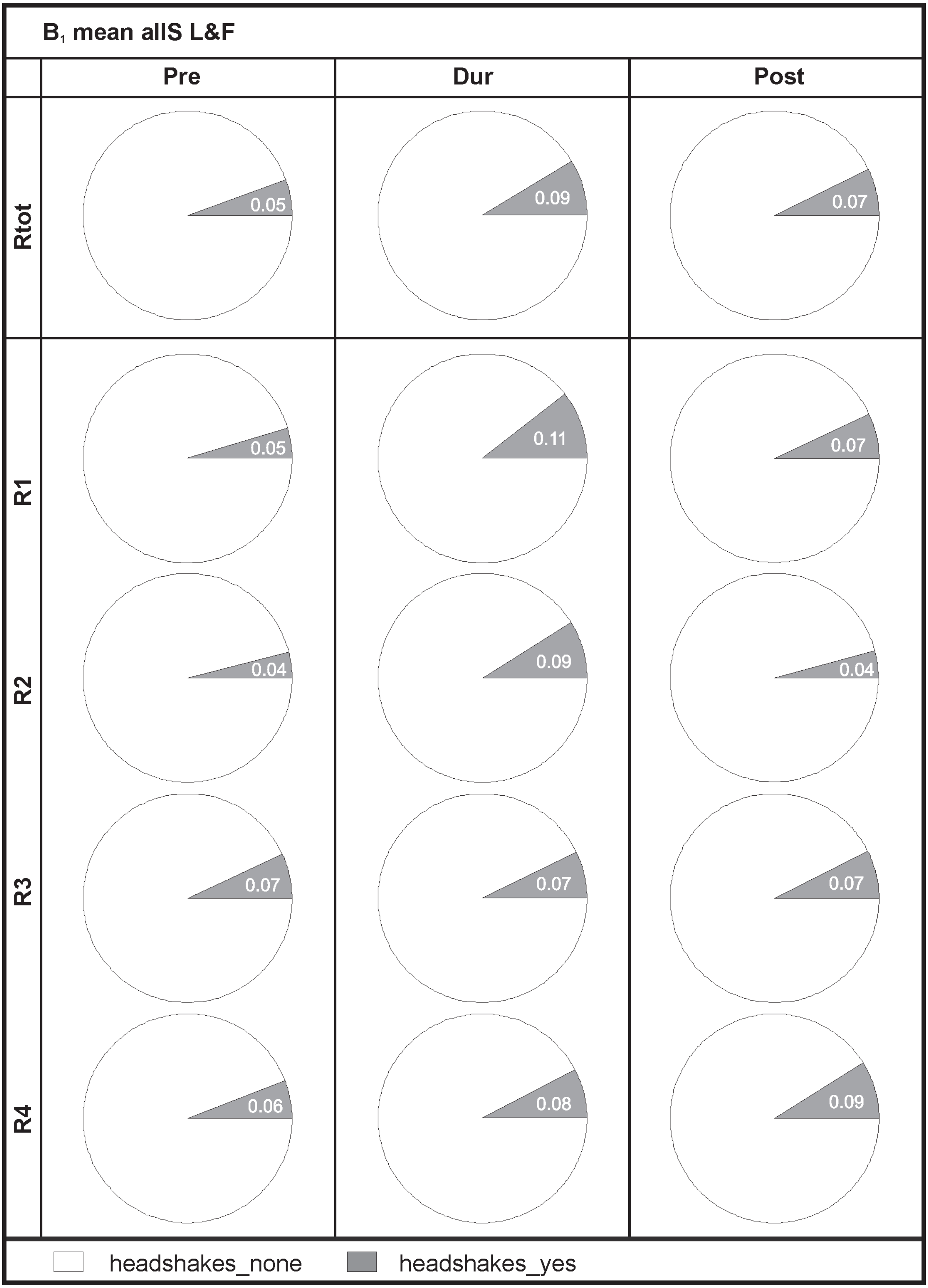


Figure 5.1-12: Dataset B_2 (1 P, S&S): Mean Distribution of Occurrence and Absence of Headshake Events before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; S&S: silent and slow; 1 P: one visitor; B_2: dataset after switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; yes/ none: headshakes occurred/ did not occur.

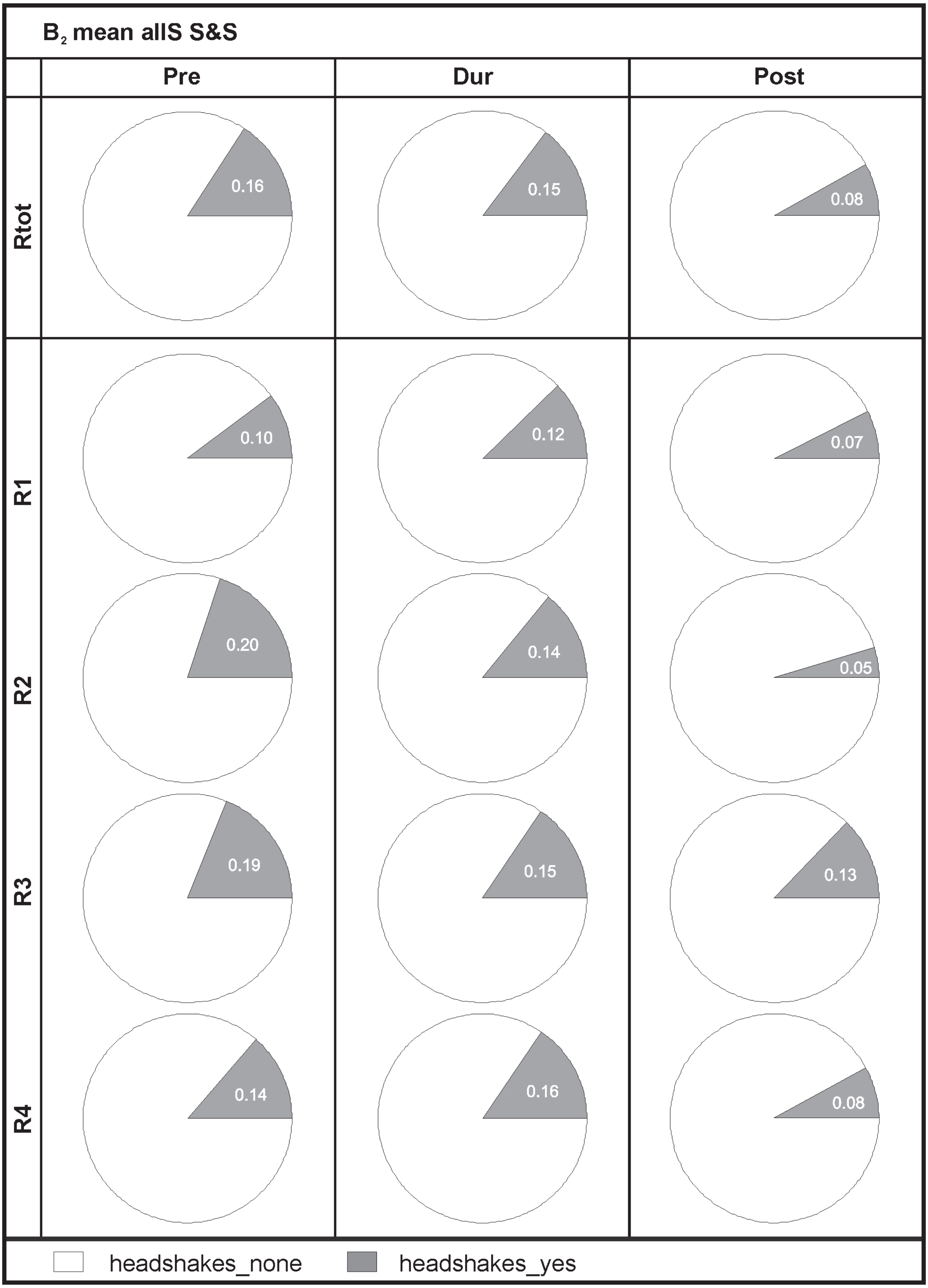


Figure 5.1.-13: Dataset C_1 (1 P, S&S): Mean Distribution of Occurrence and Absence of Headshake Events before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; S&S: silent and slow; 1 P: one visitor; C_1: dataset prior to switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; yes/ none: headshakes occurred/ did not occur.

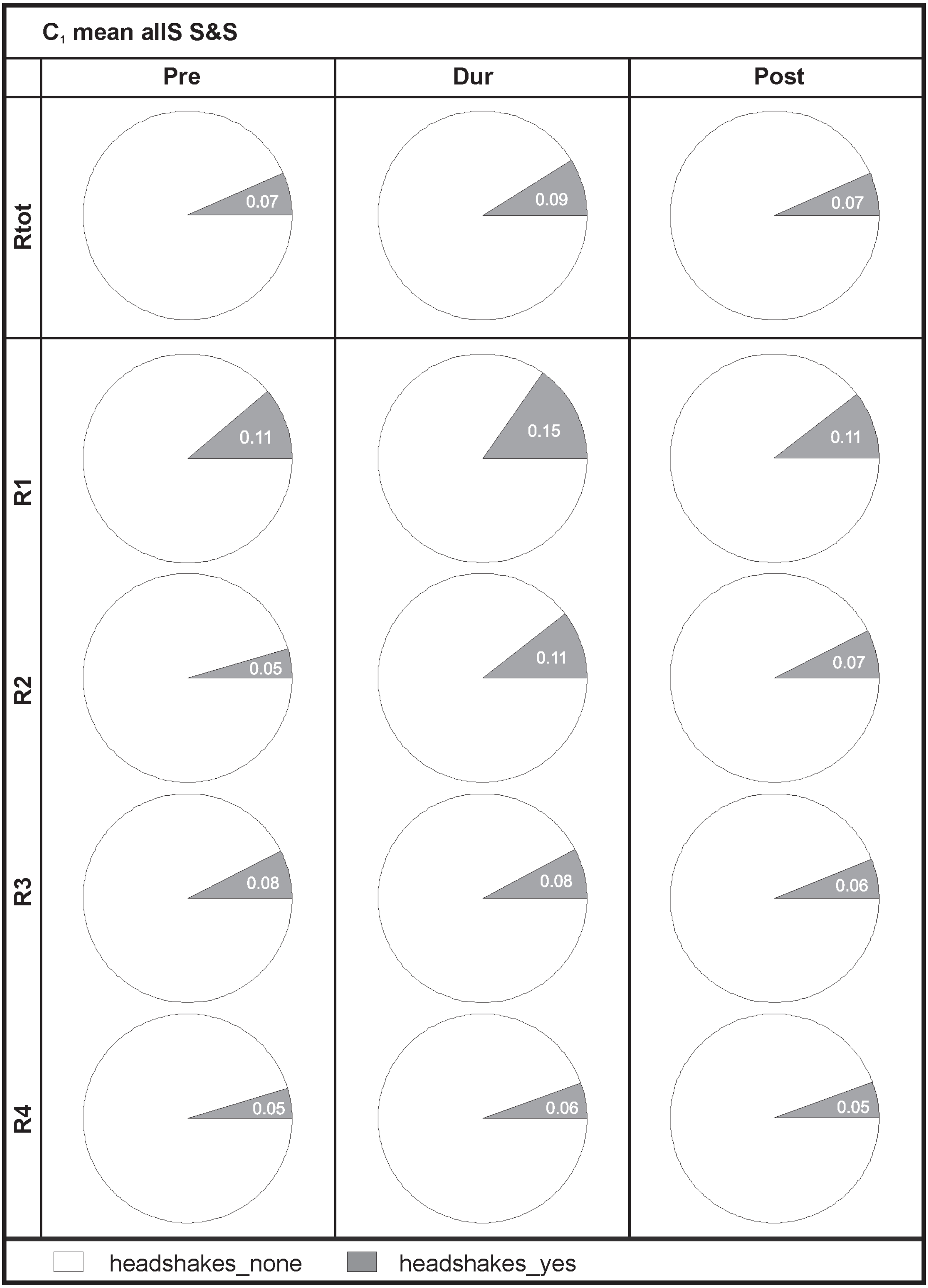


Figure 5.1-14: Dataset C_2 (1 P, L&F): Mean Distribution of Occurrence and Absence of Headshake Events before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; L&F: loud and fast; 1 P: one visitor; C_2: dataset after switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; yes/ none: headshakes occurred/ did not occur.

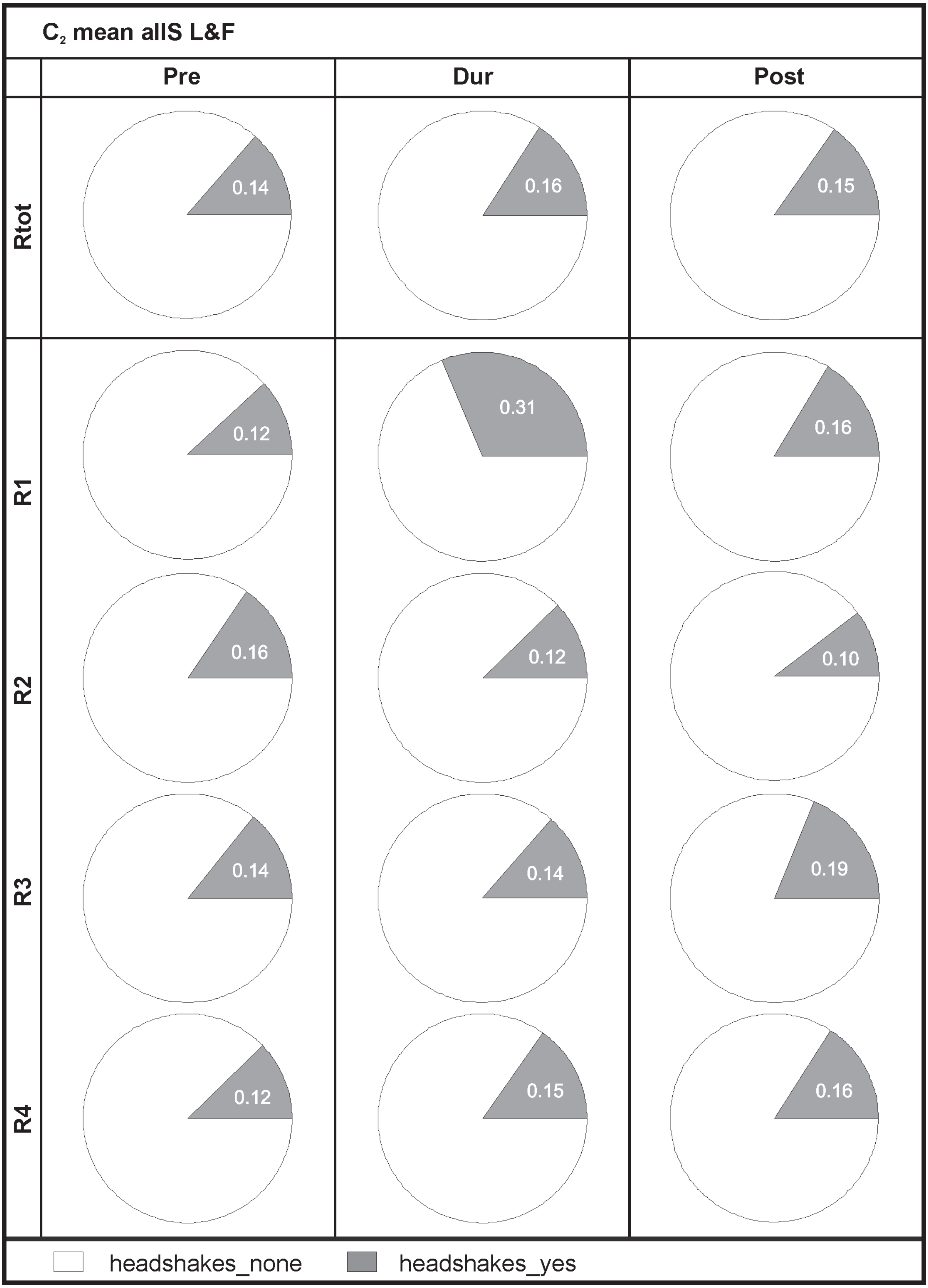


Figure 5.1-15: Group X (3 P, S&S): Mean Distribution of Occurrence and Absence of Headshake Events before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; S&S: silent and slow; 3 P: three visitors; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; yes/ none: headshakes occurred/ did not occur.

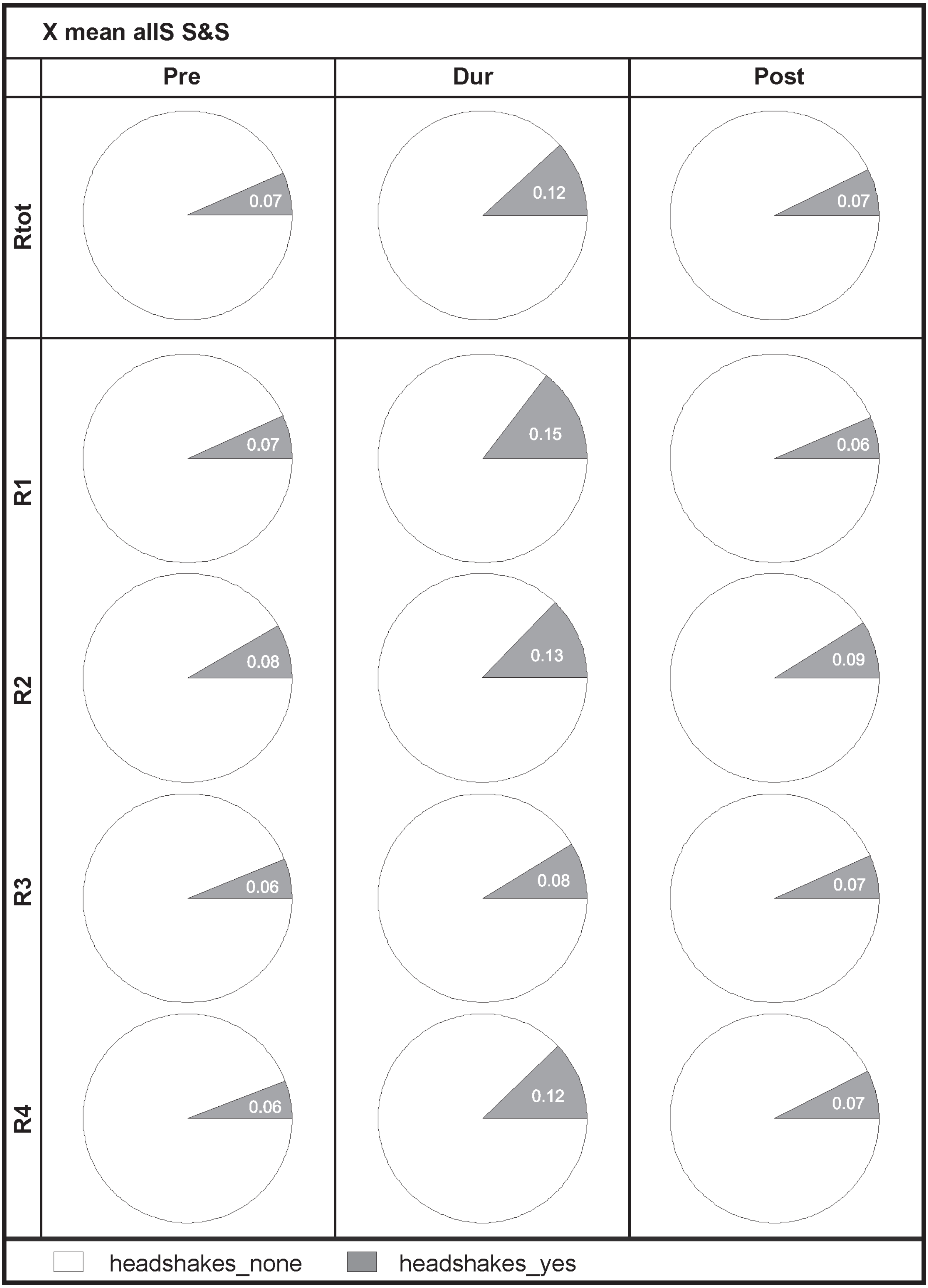
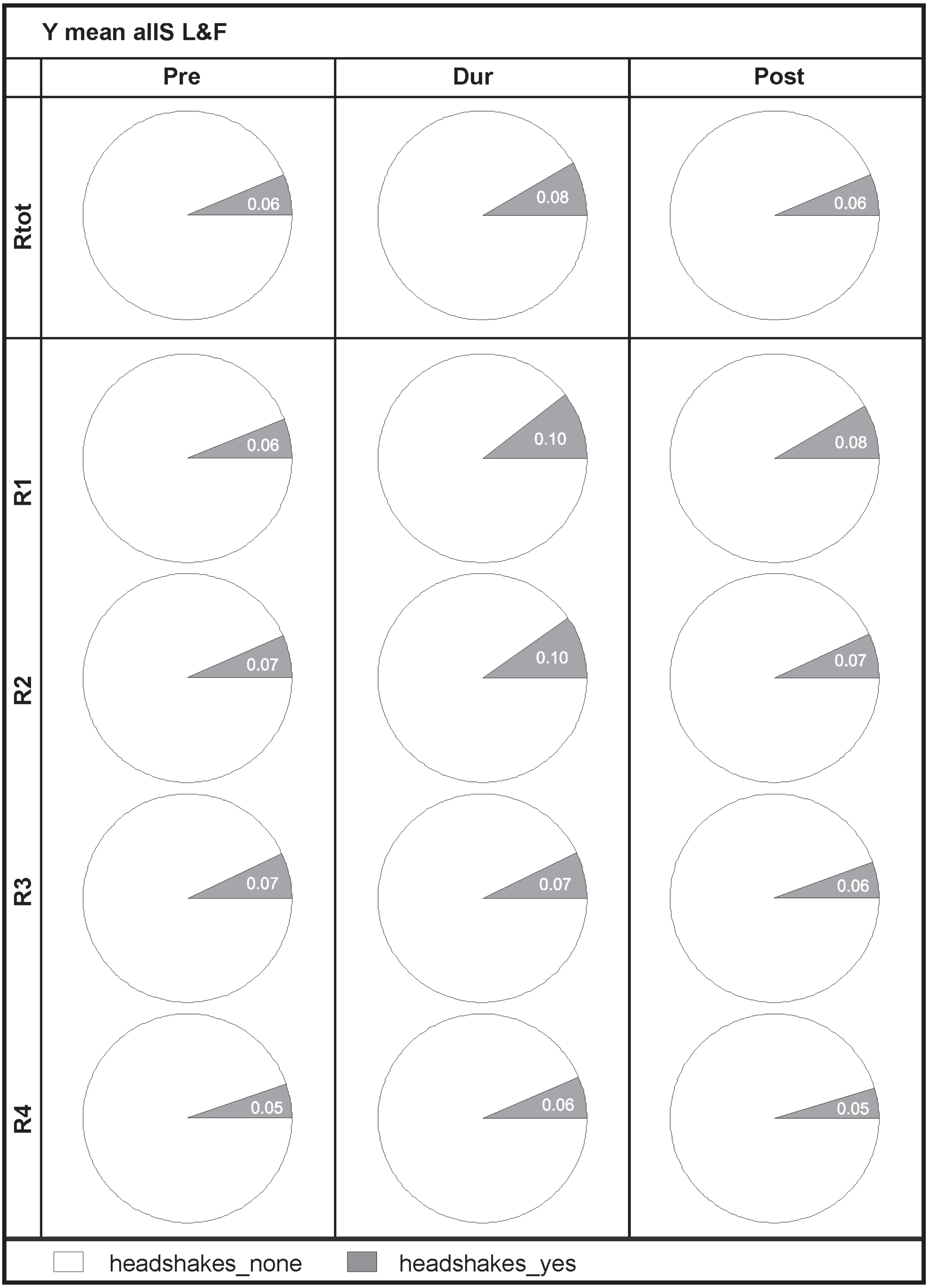


Figure 5.1-16: Group Y (3 P, L&F): Mean Distribution of Occurrence and Absence of Headshake Events before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; L&F: loud and fast; 3 P: three visitors; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; yes/ none: headshakes occurred/ did not occur.



5.1.3.4 Posture

For this passage, the reader is referred to figures 5.1-17 – 5.1-22. and table 5.1-6.

Predominant index-values in *all rows*, **all periods** (and all datasets) were calculated for the category ‘prone’ (range of median index-values: 0.87 to 0.93; for up values = 1 – prone, see tab. 5.1-6).

As for the category ‘up’, ***between-period differences*** (i.e., increases/ decreases from one period to the next) were more variable on the row level than those calculated for the entire datasets: Within-group ranges exceeded the between-group range[17] in all datasets. Most notably, changes in index-values calculated for R1 were nearly always above average, viz., in all six datasets for changes between pre- and during-visitation, and in four out of six datasets for changes between during- and post-visitation. Moreover, they showed greater differences than those calculated for the following rows in three out of the six datasets (figs. 5.1-17 – 5.1-22, tab. 5.1-6).

Before human visitation, *between-row differences* existed but did not exhibit a clear pattern (i.e., no gradients) in any of the datasets. In one out of the six datasets (dataset C_2, 1 P, L&F), R1 index-values were distinctly lower than those calculated for the other rows (fig. 5.1-20).

During and **after** human visitation, *between-row differences* were similarly frequent but did not single out any row in particular (figs. 5.1-17 – 5.1-22).

After the ***switch in visiting regime*** in groups B and C (dataset B_2: 1 P, S&S; dataset C_2: 1 P, L&F), the generally higher index-values (as compared to pre-switch) calculated for the category ‘up’ were not reflected in all rows and periods. In both groups, rows 3 and 4 contributed most to the higher index-values (see figs. 5.1-18 and 5.1-20, resp.).

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[17] for differences between pre-visit and during-visit: 0.00 to 0.03; for differences between during-visit and post-visit: -0.04 to -0.01

3. Posture

Figure 5.1-17: Dataset B_1 (1 P, L&F): Mean Distribution of Two Postures before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; L&F: loud and fast; 1 P: one visitor; B_1: dataset prior to switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; prone: lying, up: sitting/ standing.

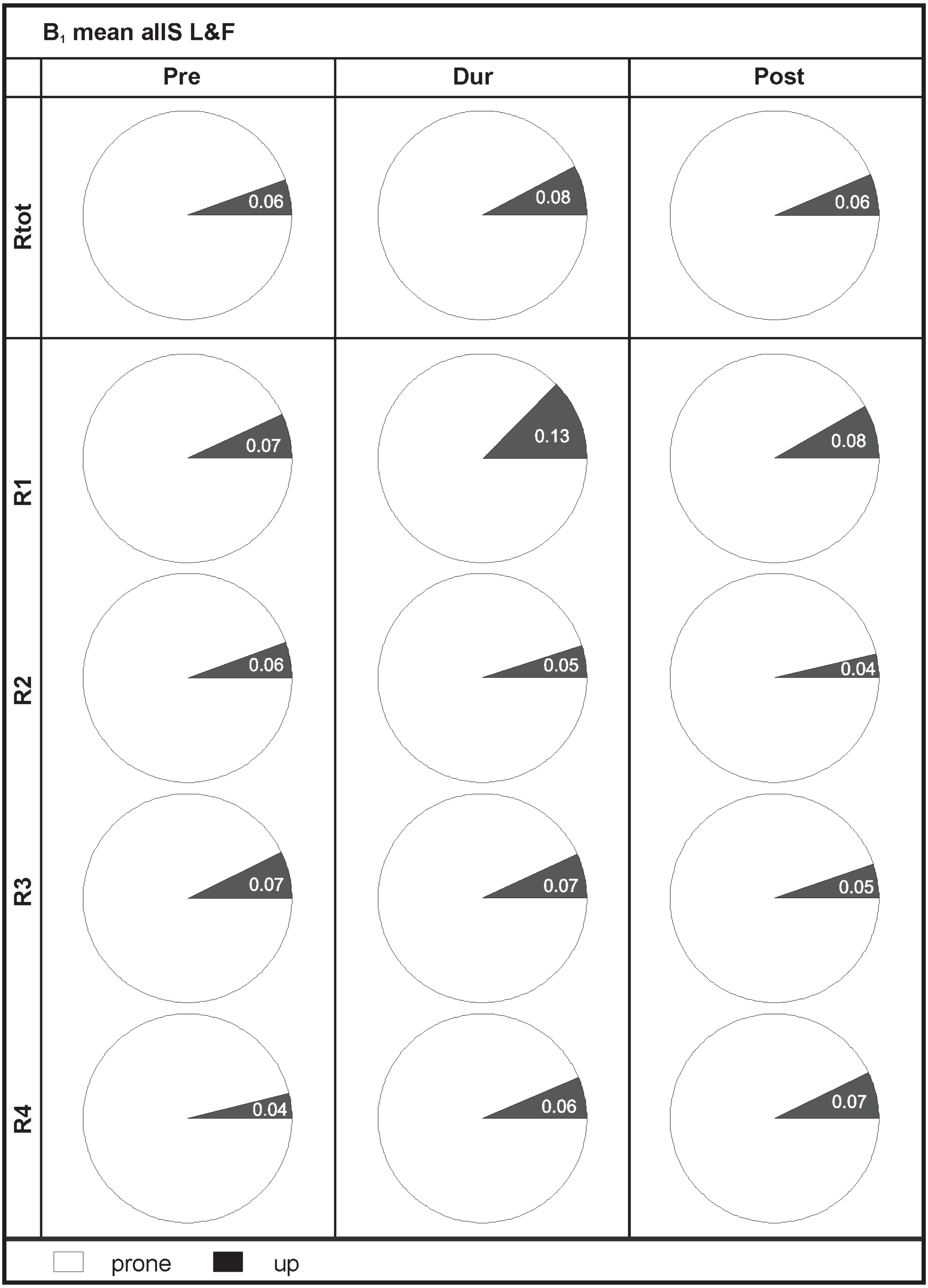


Figure 5.1-18: Dataset B_2 (1 P, S&S): Mean Distribution of Two Postures before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; S&S: silent and slow; 1 P: one visitor; B_2: dataset after switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; prone: lying, up: sitting/ standing.

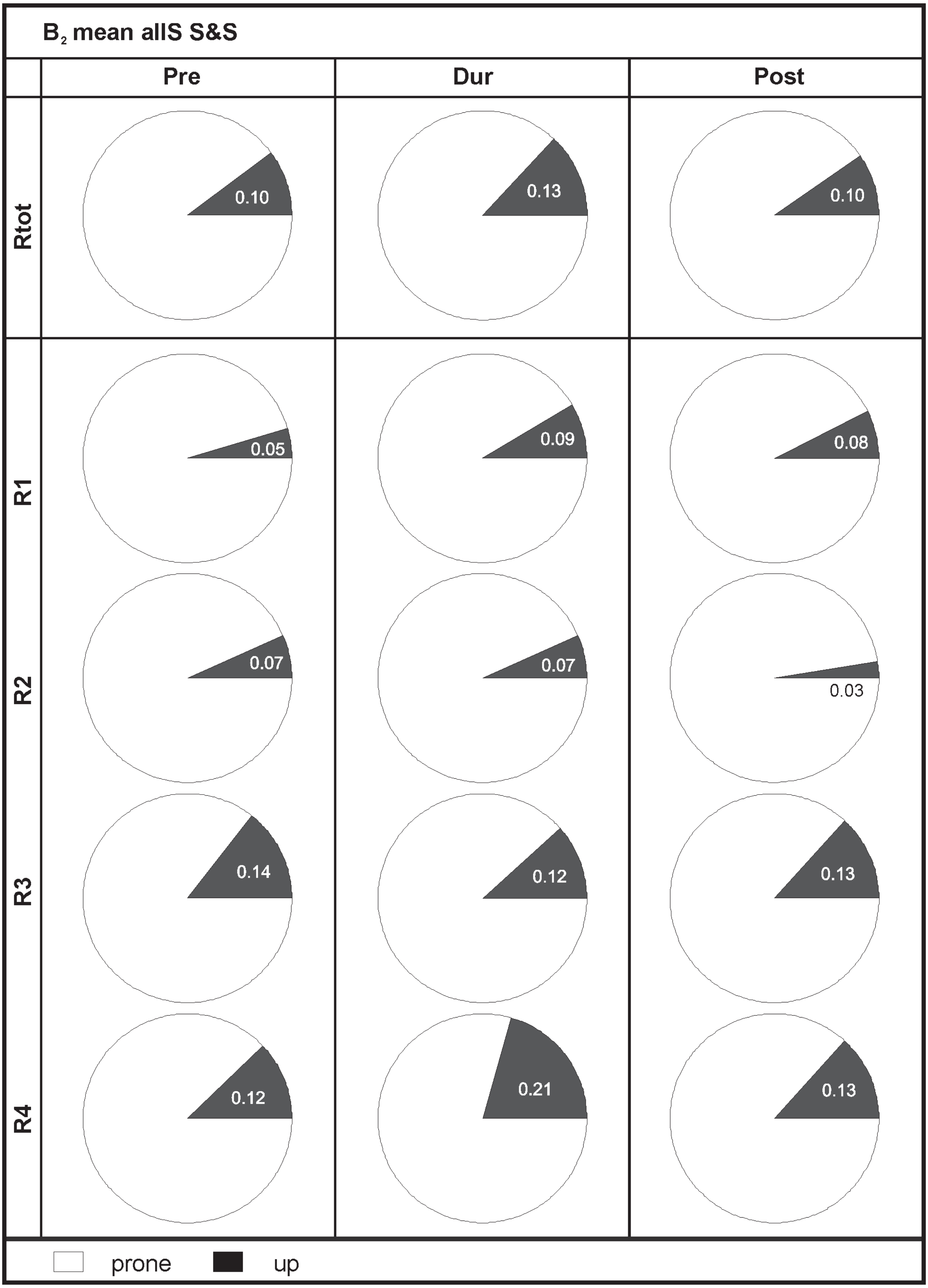


Figure 5.1-19: Dataset C_1 (1 P, S&S): Mean Distribution of Two Postures before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; S&S: silent and slow; 1 P: one visitor; C_1: dataset prior to switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; prone: lying, up: sitting/ standing.

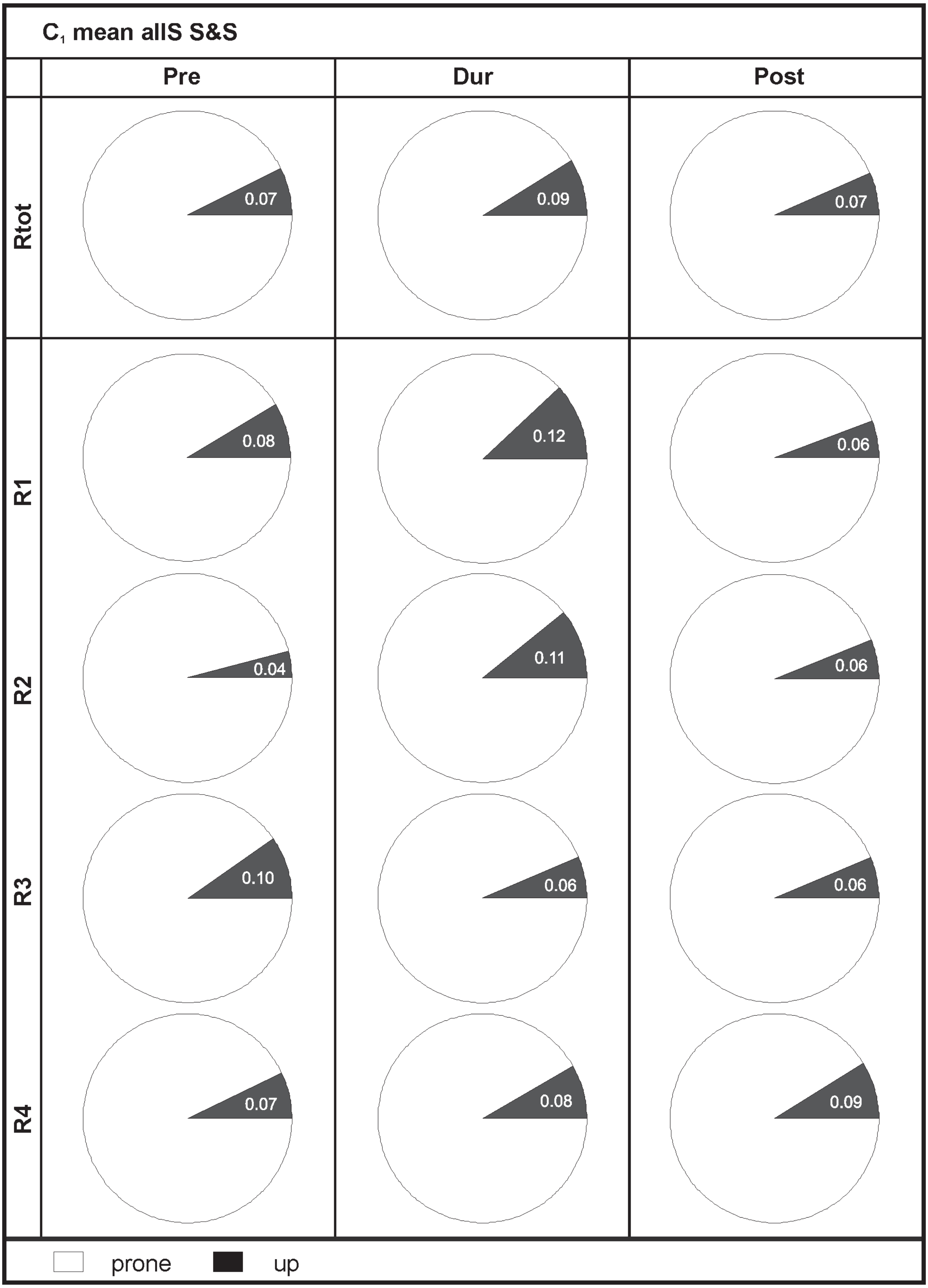


Figure 5.1-20: Dataset C_2 (1 P, L&F): Mean Distribution of Two Postures before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; L&F: loud and fast; 1 P: one visitor; C_2: dataset after switch in visiting regime; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; prone: lying, up: sitting/ standing.

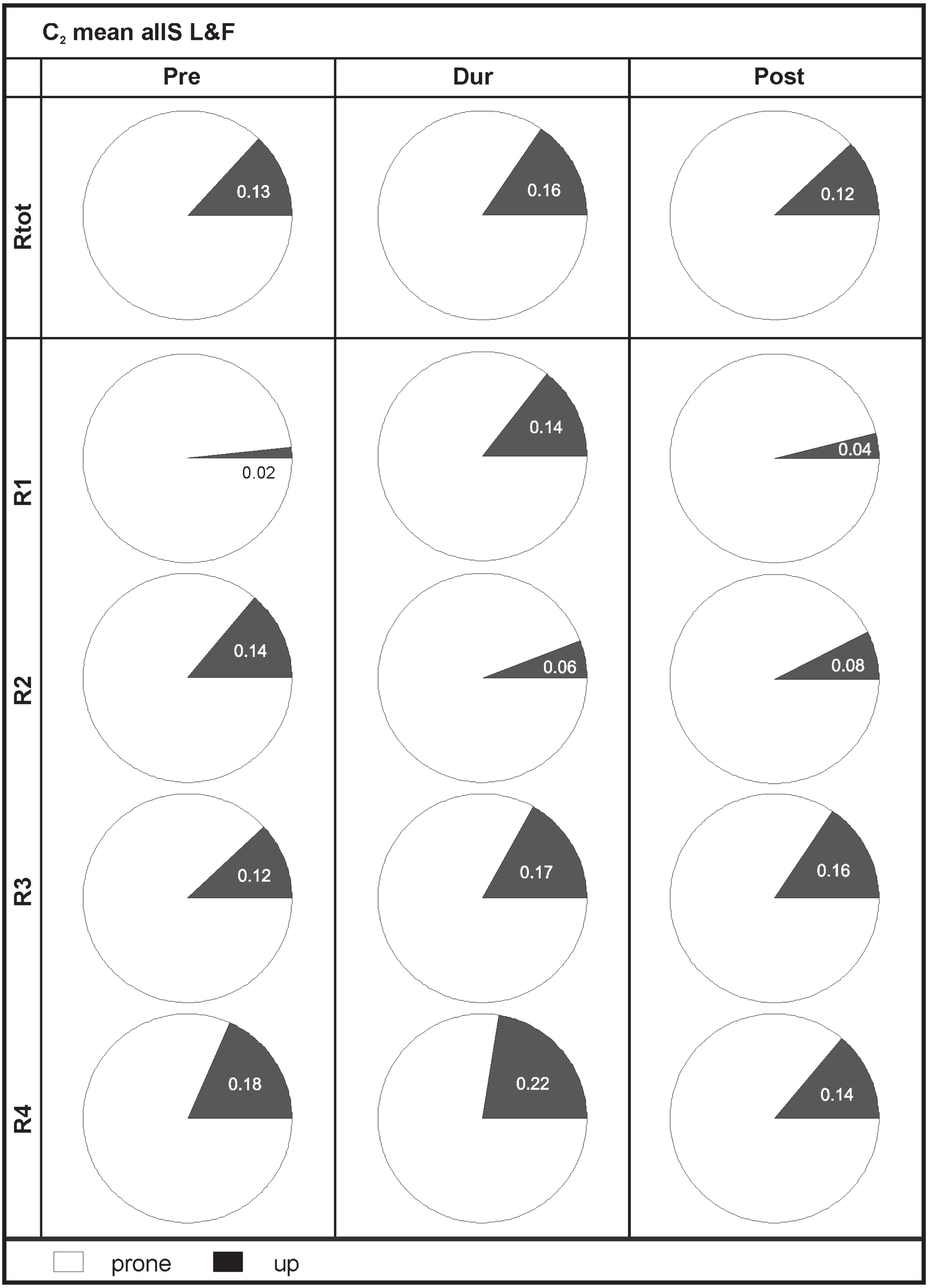


Figure 5.1-21: Group X (3 P, S&S): Mean Distribution of Two Postures before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; S&S: silent and slow; 3 P: three visitors; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; prone: lying, up: sitting/ standing.

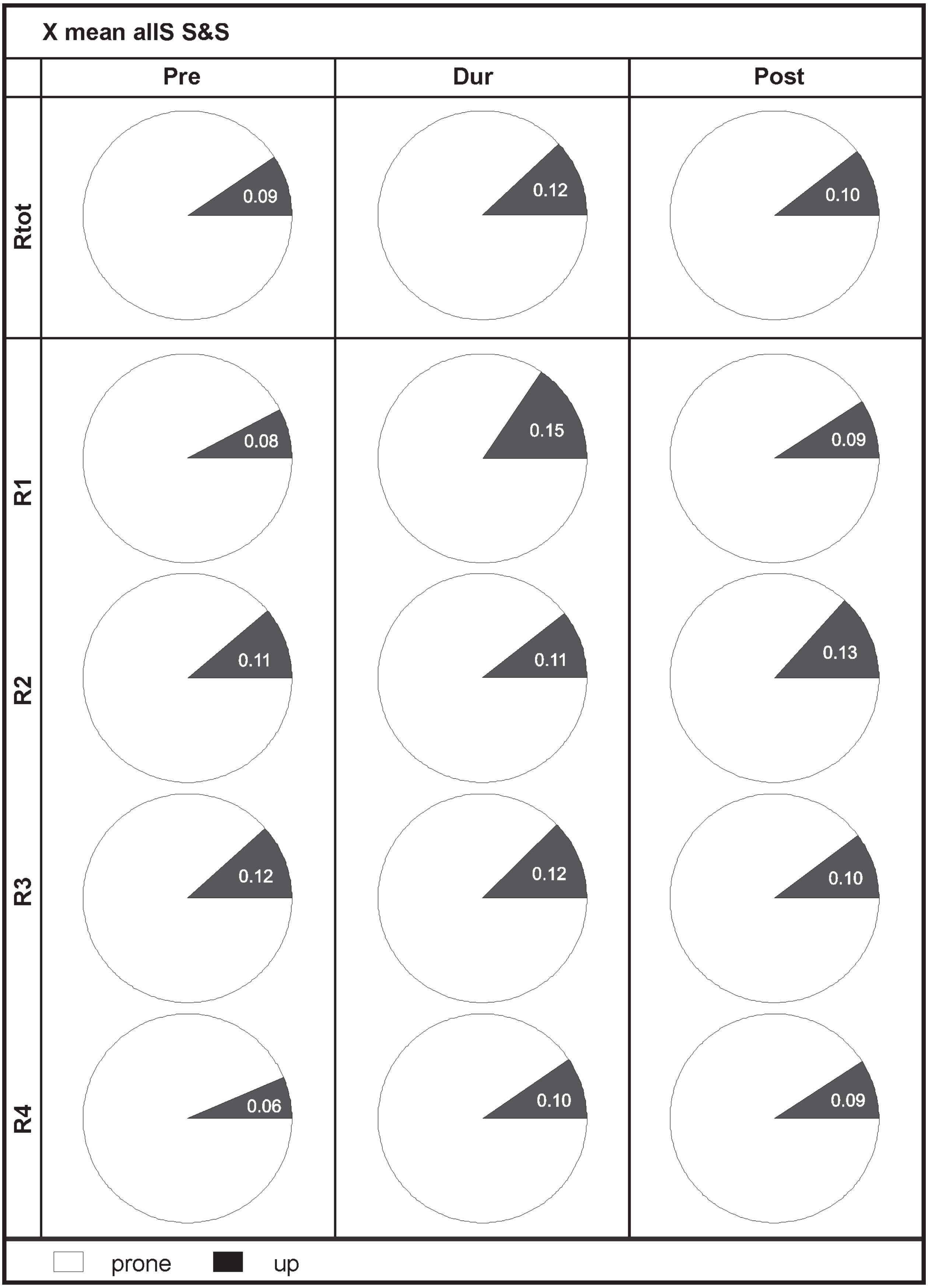
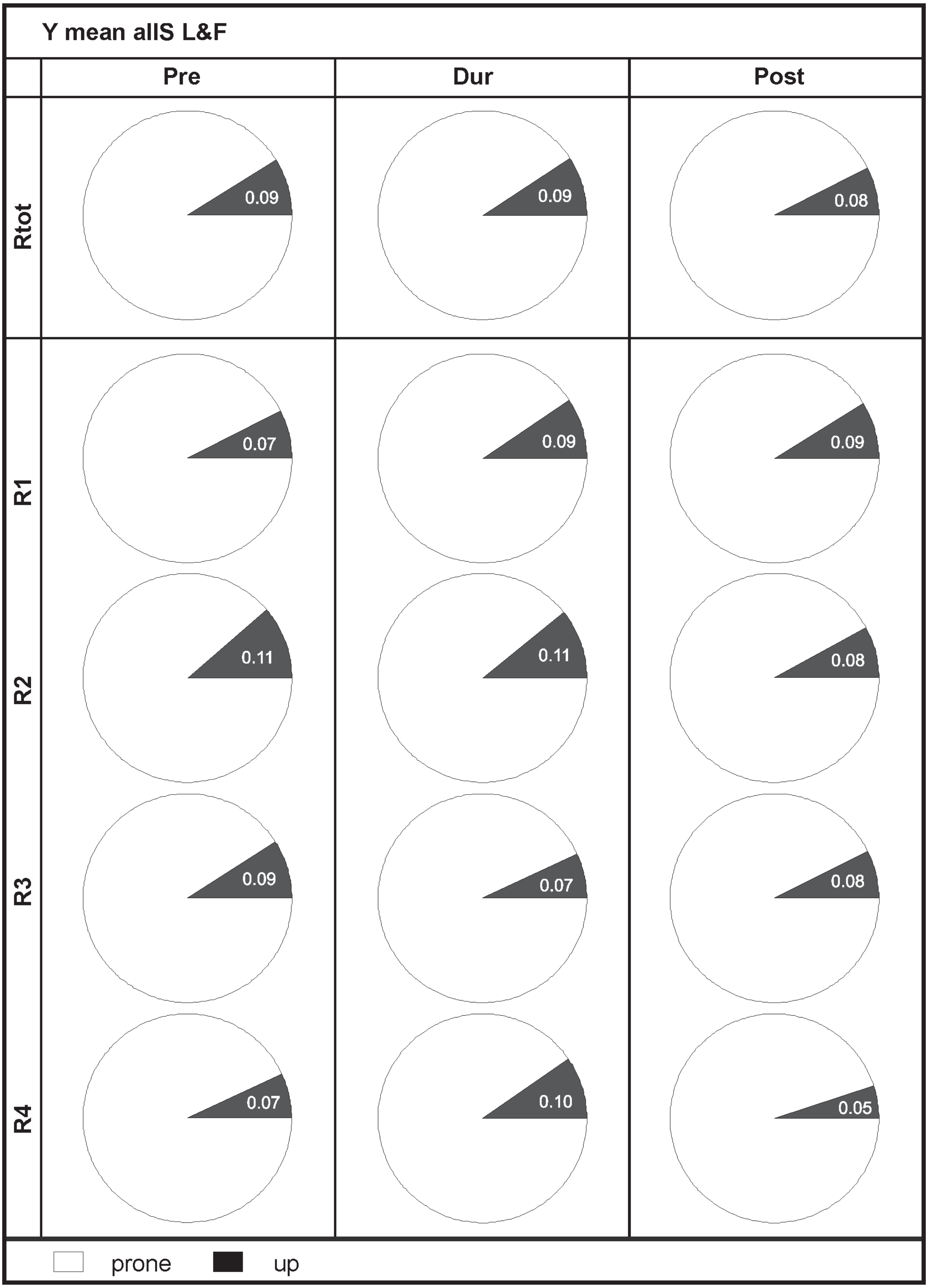


Figure 5.1-22: Group Y (3 P, L&F): Mean Distribution of Two Postures before, during, and after Human Visitation for All Rows Together, and Separately for Each Row. allS: all sessions per dataset; L&F: loud and fast; 3 P: three visitors; Rtot: sum across all four rows; R1: first row, R2: second row, R3: third row, R4: fourth row; prone: lying, up: sitting/ standing.



5.1.3.5 Friedman-Tests

The amount of variation visible between the rows necessitated **tests for statistical significance**. For this, row data were subjected to **global Friedman-tests** (difference between any of the rows), followed by pair-wise Friedman-tests whenever the global test indicated a significant difference among the rows. Global Friedman-tests were calculated separately for each dataset and period, for the categories[18] ‘alert’, ‘rest&Co’, ‘occurrence of headshakes_yes’, and ‘up’. Although global Friedman-tests detected differences in several cases, **pair-wise tests** (Holm-Bonferroni-method → sequentially adjusted significance; see chapter 4.4.2.3.5) were statistically significant ($\alpha_F = 5\ \% = \alpha_{V,\ 6\ \text{comparisons}} = 0.0083$) in two cases only, viz., differences during visits between R1 and R4 for ‘alert’ as well as ‘rest&Co’ in dataset B_1 (1 P, L&F). The overall lack of significant differences permitted rows of a given dataset to be pooled (R_{tot}) and the dataset to be examined as a whole.

5.1.4 Relationship between Intensity of Group Responses and ‘Type of Disturbance’

It could be demonstrated for all aspects (behaviour states: ‘alert’, ‘rest&Co’; behaviour event: ‘occurrence of headshakes_yes’; and posture: ‘up’) and all datasets examined that the focal groups’ reactions **during** human visitation differed from those shown **prior to** and **after** visitation. The magnitude of the differences found, however, was very variable with respect to the datasets as well as to the parameters examined.

The following section, therefore, investigates in detail in how far this was related to the type of disturbance the groups had been subjected to during human visitation (i.e., different visiting regimes) and/or the extent of ‘omnipresent’ conspecific presence.

As described in chapter 4.3.4.2 (also see fig. 3-25), all **visiting regimes** followed the **same time schedule**. The visitor(s) started to walk towards the penguin group at a distance of 20-25 m[19] from the colony edge. At pre-set distances (15 m, 5 m, and 3 m, respectively), the visitor(s) stayed for approximately 2 min before moving on to the next stop (from 15 m to 5 m, from 5 m to 3 m), or retreating (from 3 m). Retreat to the initial distance (20-25 m) occurred in a straight line at the same pace as the approach and without any in-between stops.

In contrast, the extent and intensity of **conspecific presence** had not been manipulated.

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[18] Having found little consistent differences with respect to the remaining behaviour states, these were excluded from analyses.

[19] Maximum distance depended upon geography, i.e. the visitor(s) followed the foot line of the hill opposite the colony until they could approach the focal group in a straight line.

For the four parameters that had exhibited sensitivity towards human disturbance on the level of focal groups (behaviour states: ‘alert’, ‘rest&Co’; behaviour event: ‘occurrence of headshakes_yes’; and posture: ‘up’), the following **questions** were **addressed**:

- Did group responses correlate with impact of conspecific presence outside human visitation (before and after) – and if so, how strong was that relationship (section 5.1.4.1)?
- Did group responses correlate with impact of conspecific presence during human visitation – and if so, how strong was that relationship (section 5.1.4.2)?
- Did group responses correlate with impact of human visitation – and if so, how strong was that relationship (section 5.1.4.3)?
- How did results obtained with respect to impact of conspecific presence compare to those on impact of human visitation (section 5.1.4.4)?

5.1.4.1 Impact of Conspecific Presence on Focal-Group Behaviour outside Human Visitation

5.1.4.1.1 Section Summary

Impact of conspecific presence did not tally with either absolute or proportional numbers of conspecifics observed (see figs. 5.1-23 a, b) in that generally higher numbers of conspecifics present (e.g., dataset C_2) did not result in generally higher r^2-values for any of the parameters examined.

Between periods (pre-, post-), the impact of conspecific presence was extremely variable for any given parameter and in all datasets. If r^2-values crossed the 10 % threshold at all, they did so *either* before *or* after human visitation, but never for both periods within the same dataset-parameter combination (see tabs. 5.1-8, 5.1-9; e.g., group X ‘alert’: pre-, but not post-visit; dataset B_2 ‘rest&Co’: post-, but not pre-visit).

Prior to visitation (but not after), responses of group X (3 P, S&S) were most strongly (of all datasets) correlated with conspecific presence for all parameters examined (max. r^2-alert: 0.430; max. r^2-rest&Co: 0.490_{inverse}; max. r^2-headshakes_yes: 0.376; max. r^2-up: 0.310). **After** visitation, maximum correlations were lower and spread across datasets (max. r^2-alert: 0.253 for dataset B_2, 1 P, S&S; max. r^2-rest&Co: 0.230_{inverse} for dataset C_1, 1 P S&S; max. r^2-headshakes_yes: 0.171_{inverse} for group Y, 3 P, L&F; max. r^2-up: 0.157_{inverse}, likewise for group Y).

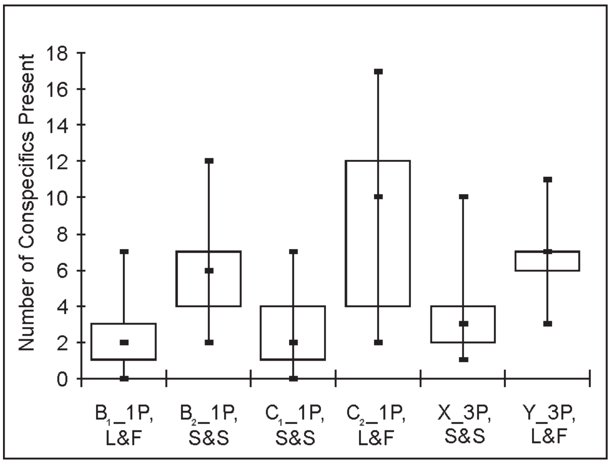
Upon occurrence, conspecific presence was always positively correlated with the category ‘alert’, while it was invariably negatively correlated with the category ‘rest&Co’. In contrast, no consistent directional relationship was found as regards the remaining two categories, although positive correlations were more frequent.

Results show that conspecific presence may represent a ‘potent’ source of influence in the absence of human visitors. It therefore seemed prudent to examine any conspecific influence during human visitation prior to assessing the impact of human visitation itself. In order to do so, the influence of the variable ‘human visitation’ in relation to the influence of conspecifics needed further investigation. With respect to the period ‘during-visitation’, this was effected by partialling out one influence while examining the other (see following sections).

Following, results are presented in detail.

Prior to examining the impact of human visitation, conspecific presence was compared between the datasets using all sampling points available per dataset (i.e., regardless of human presence/ absence). Conspecific presence was visualised in two ways, viz., in absolute numbers (as captured in the Point Performance Indicator Value, PPIV-C; fig. 5.1-23 a), and as a proportion of focal group size in order to obtain a group-size independent estimate (fig. 5.1-23 b).

As becomes evident, conspecific presence varied greatly between the datasets in both median and range. Even if conspecifics were proportionalised according to group size (fig. 5.1-23 b), both datasets 2 (datasets B_2 and C_2 → after the switch in visiting regimes) remained considerably set off from the others, particularly with respect to higher medians. Additionally, within-group variability as well as maximum numbers were greatest at dataset C_2 (1 P, L&F).



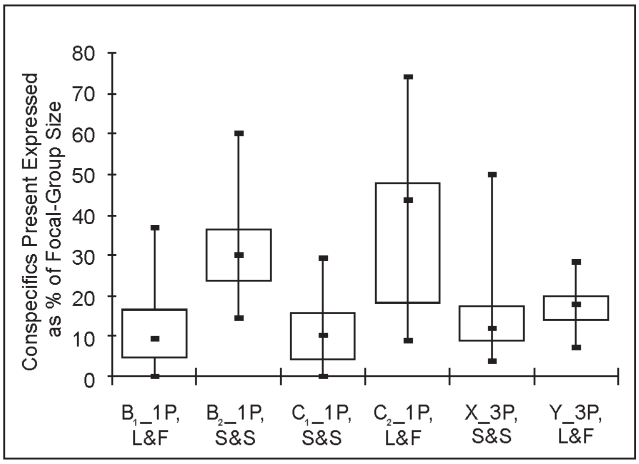


Figure 5.1-23 a: Distribution of Conspecifics Present (Absolute Numbers, All Sampling Points). Boxplots show minimum, 1st quartile, median, 3rd quartile, and maximum values. B, C, X, Y: focal groups; B_1/ B_2, C_1/ C_2: different datasets obtained from the same focal group prior to and after a switch in visiting regime; 1 P: one visitor, 3 P: three visitors; S&S: silent and slow, L&F: loud and fast.

Figure 5.1-23 b: Distribution of Conspecifics Present Expressed as a Proportion of Focal-Group Size. Boxplots show minimum, 1st quartile, median, 3rd quartile, and maximum proportional values. B, C, X, Y: focal groups; B_1/ B_2, C_1/ C_2: different datasets obtained from the same focal group prior to and after a switch in visiting regime; 1 P: one visitor, 3 P: three visitors; S&S: silent and slow, L&F: loud and fast.

5.1.4.1.2 Spearman's Rank Correlations between Conspecific Presence and Focal-Group Behaviour before and after Human Visitation

The periods before (pre-) and after (post-) human visitation were used to assess to which extent the presence of conspecifics influenced the incubating birds' behaviour. Correlations (Spearman's rho) were computed between conspecific presence (obtained by Point Performance Indicator Value for Conspecific Presence, PPIV-C) and the four behaviour parameters listed in table 5.1-7.

Table 5.1-7: **Variables for which Correlations were Computed between Conspecific Presence and Focal-Group Behaviour before, resp. after Human Visitation.** PPIV-C: Point Performance Indicator Value for Conspecific Presence; correlations: Spearman's rho.

Variable 1 (PPIV-C)	Variable 2
total number of conspecifics present before/ after human visitation	alert (behaviour state)
	rest&Co (behaviour state)
	headshakes_yes (behaviour event)
	up (posture)

Results on all four parameters are summarised in table 5.1-8 and presented in detail in table 5.1-9. Correlations (r) have been squared to show the percentage of variance explained (r^2).

N.b.: As introduced in chapter 4.4.2.3) and repeated in section 5.1.1, classed proportions of explained variance (r^2) and levels of significance (p) have been colour-coded (tabs. 5.1-3 and 5.1-4). Tendentially significant r^2-values are given in *italics*, and r^2-values based on inverse correlations are given in **boldface**. Non-significant values are marked as 'n.s.' (tab. 5.1-8; tab. 5.1-9). Significant results were considered biologically relevant, if the amount of variance explained equalled at least 10 % (in tab. 5.1-9: r^2-values = 0.100).

Table 5.1-8: Overview – Variance in Four Parameters of Focal-Group Behaviour as Explained by Conspecific Presence before and after Human Visitation. pre-visit: before human visitation; post-visit: after human visitation; alert: birds vigilant, rest&Co: birds non-committal, headshakes_yes: headshakes happened, up: birds sitting or standing; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; pos: positive correlation; **inv:** inverse correlation; n.s.: correlation not significant; *italics:* correlation tendentially significant; coloured cells: r^2-values exceeding 10 % of explained variance; correlations: Spearman's rho.

Conspecific Presence Pre-Visit	**B_1**	**B_2**	**C_1**	**C_2**	**X**	**Y**
Alert	pos	n.s.	pos	pos	pos	pos
Rest&Co	**inv**	n.s.	***inv***	**inv**	**inv**	**inv**
Headshakes_yes	n.s.	n.s.	**inv**	n.s.	pos	n.s.
Up	pos	pos	**inv**	*pos*	pos	n.s.
Conspecific Presence Post-Visit	**B_1**	**B_2**	**C_1**	**C_2**	**X**	**Y**
Alert	pos	pos	pos	n.s.	n.s.	n.s.
Rest&Co	**inv**	**inv**	**inv**	n.s.	n.s.	n.s.
Headshakes_yes	n.s.	n.s.	n.s.	pos	pos	**inv**
Up	n.s.	n.s.	pos	pos	n.s.	**inv**

Table 5.1-8 suggests conspecific presence to influence focal-group behaviour outside human visitation, with mainly positive (or non-significant, but not inverse) correlations found as regards the parameter 'alert', and mainly inverse (or non-significant, but not positive) correlations obtained with respect to the parameter 'rest&Co'. The parameters 'headshakes_yes' (pre-visit: mainly non-significant; post-visit: non-significant in half of the datasets) and 'up' (pre-visit: mainly positive; post-visit: non-significant in half of the datasets), appeared to be less affected by conspecific presence, particularly post-visit, and response directions (positive: increasing with rising numbers of conspecifics present; inverse: decreasing with rising numbers of conspecifics present) differed between datasets for which significant correlations had been obtained.

The following passages briefly list for each parameter in turn the significant results for which the amount of variance explained equalled at least 10 %; all values are provided in table 5.1-9.

Behaviour states: Prior to visitation, conspecific presence accounted for more than 10 % of the variance of the parameter 'alert' in three of the six datasets, viz., B_1 (approx. 13 %), C_2 (27 %) and X (43 %). **After** the visits, it was found to have an impact on vigilance behaviour in datasets B_2 (approx. 25 %) and C_1 (approx. 21 %). In both periods, increased conspecific presence resulted in increased vigilance.

Table 5.1-9: Percentage of Variance in Four Parameters of Focal-Group Behaviour as Explained by Conspecific Presence before and after Human Visitation. alert: birds vigilant, rest&Co: birds non-committal, headshakes_yes: headshakes happened, up: birds sitting or standing; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; 1 P: one visitor, 3 P: three visitors; L&F: loud and fast, S&S: silent and slow; pre: before human visitation, post: after human visitation; r^2: r-square-values (percentage of explained variance); p: significance (two-tailed); t: number of sampling points; n.s.: not significant; *italics*: correlation only tendentially significant; **boldface**: inverse correlation; correlations: Spearman's rho.

	Dataset	Number of Sessions	Period	r^2	p	t
Alert	B_1_1 P_L&F	8	pre	0.127	0.000	139
	B_2_1 P_S&S	3		n.s.	0.849	46
	C_1_1 P_S&S	6		0.081	0.004	101
	C_2_1 P_L&F	3		0.270	0.000	58
	X_3 P_S&S	5		0.430	0.000	87
	Y_3 P_L&F	5		0.081	0.004	99
	B_1_1 P_L&F	8	post	0.064	0.001	186
	B_2_1 P_S&S	3		0.253	0.000	66
	C_1_1 P_S&S	6		0.213	0.000	114
	C_2_1 P_L&F	3		n.s.	0.214	66
	X_3 P_S&S	5		n.s.	0.493	119
	Y_3 P_L&F	5		n.s.	0.678	99
Rest & Co	B_1_1 P_L&F	8	pre	**0.162**	0.000	139
	B_2_1 P_S&S	3		n.s.	0.716	46
	C_1_1 P_S&S	6		***0.038***	*0.051*	101
	C_2_1 P_L&F	3		**0.171**	0.001	58
	X_3 P_S&S	5		**0.490**	0.000	87
	Y_3 P_L&F	5		**0.096**	0.002	99
	B_1_1 P_L&F	8	post	**0.061**	0.001	186
	B_2_1 P_S&S	3		**0.141**	0.002	66
	C_1_1 P_S&S	6		**0.230**	0.000	114
	C_2_1 P_L&F	3		n.s.	0.692	66
	X_3 P_S&S	5		n.s.	0.208	119
	Y_3 P_L&F	5		n.s.	0.151	99
Headshakes_yes	B_1_1 P_L&F	8	pre	n.s.	0.694	131
	B_2_1 P_S&S	3		n.s.	0.960	46
	C_1_1 P_S&S	6		**0.046**	0.038	95
	C_2_1 P_L&F	3		n.s.	0.131	54
	X_3 P_S&S	5		0.376	0.000	87
	Y_3 P_L&F	5		n.s.	0.310	97
	B_1_1 P_L&F	8	post	n.s.	0.500	186
	B_2_1 P_S&S	3		n.s.	0.401	63
	C_1_1 P_S&S	6		n.s.	0.214	113
	C_2_1 P_L&F	3		0.066	0.038	66
	X_3 P_S&S	5		0.054	0.011	118
	Y_3 P_L&F	5		**0.171**	0.000	97
Up	B_1_1 P_L&F	8	pre	0.130	0.000	139
	B_2_1 P_S&S	3		0.270	0.000	46
	C_1_1 P_S&S	6		**0.071**	0.007	101
	C_2_1 P_L&F	3		*0.062*	*0.061*	58
	X_3 P_S&S	5		0.310	0.000	87
	Y_3 P_L&F	5		n.s.	0.634	99
	B_1_1 P_L&F	8	post	n.s.	0.995	186
	B_2_1 P_S&S	3		n.s.	0.381	66
	C_1_1 P_S&S	6		0.034	0.050	114
	C_2_1 P_L&F	3		0.079	0.002	66
	X_3 P_S&S	5		n.s.	0.390	119
	Y_3 P_L&F	5		**0.157**	0.000	99

The parameter ‘rest&Co’ was inversely affected (i.e., an increase in conspecific presence led to a decrease in non-committal behaviours) in the same datasets and during the same periods. The relationship was strongest at group X (pre; 49 %) and weakest at dataset B_2 (post; approx. 14 %).

Behaviour event: Conspecific presence **before** human visitation explained approximately 38 % of the variance found for the parameter ‘headshakes_yes’ in group X, but did not ‘cross the 10 % threshold’ in any of the other datasets. **After** human visitation, it accounted for approximately 17 % of the variation explained at group Y (1 P, L&F; inverse relationship), and likewise failed to pass the threshold in the other datasets.

Posture: Prior to human visitation, conspecific presence explained 13 %, 27 % and 31 % of the variance found for the parameter ‘up’ in datasets B_1, B_2, and X, respectively. **After** human visitation, it did not feature greatly in any of these datasets, but accounted for approximately 16 % of the variance explained at group Y. In contrast to findings prior to human visitation, however, the latter relationship was based on an inverse correlation.

5.1.4.2 Impact of Conspecific Presence during Human Visitation on Focal-Group Behaviour

5.1.4.2.1 Section Summary

Focal-group evaluations did not detect a consistent linear relationship between conspecific presence and human visitation.

Results show that conspecific presence continued to represent a ‘potentially potent’ source of influence in the presence of human visitors. Similar to before and after visitation, the parameters ‘alert’ (positive) and ‘rest&Co’ (inverse) retained their respective response directions during visitation, while no consistent directional relationship was found as regards the categories ‘headshakes_yes’ and ‘up’.

Particularly with respect to the parameters ‘alert’ and ‘rest&Co’, it was necessary to eliminate any conspecific influence prior to assessing the impact of human visitation. As it had been impossible to bodily remove conspecifics from the scene before human(s) went out to visit a focal group, elimination of conspecific impact was effected post-recording, by calculating partial correlations during data analyses.

Following, results are presented in detail.

5.1.4.2.2 Partial Rank Correlations of Conspecific Presence and Focal-Group Behaviour during Human Visitation

To examine conspecific impact during human visitation, influence of human visitor(s) was eliminated by calculating partial rank correlations (Spearman’s rho) for the variables presented in table 5.1-10.

Prior to partial rank correlations, however, the relationship between **human visitation and conspecific presence** was examined (calculating ‘full’[20] correlations, i.e., correlation between PPIV-C and PPIV-H) to see whether conspecific influence on focal-groups might actually be mediated by human impact on these conspecifics. Focal-group evaluations detected **no consistent linear relationship** in any of the datasets (Spearman’s rho all two-tailed $p >> 0.05$).

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[20] as opposed to partial…

Table 5.1-10: Variables for which Partial Rank Correlations were Computed between Conspecific Presence during Human Visitation and Focal-Group Behaviour (with Human Visitation Partialled out). partial rank correlations: Spearman's rho.

Variable 1 (PPIV-C)	Variable 2
total number of conspecifics present during human visitation	alert (behaviour state)
	rest&Co (behaviour state)
	headshakes_yes (behaviour event)
	up (posture)

Results on partial rank correlations between conspecific presence and the four behaviour parameters are summarised in table 5.1-11 and presented in detail in table 5.1-12.

N.b.: As introduced in chapter 4.4.2.3 and repeated in section 5.1.1, classed proportions of explained variance (r^2) and levels of significance (p) have been colour-coded (tabs. 5.1-3 and 5.1-4). Tendentially significant r^2-values are given in *italics*, and r^2-values based on inverse correlations are given in **boldface**. Non-significant values are marked as 'n.s.' (tab. 5.1-11; tab. 5.1.-12). Significant results were considered biologically relevant, if the amount of variance explained equalled at least 10 % (in tab. 5.1-12: r^2-values = 0.100).

Table 5.1-11: Overview – Variance in Four Parameters of Focal-Group Behaviour as Explained by Conspecific Presence during Human Visitation (with Human Visitation Partialled out). alert: birds vigilant, rest&Co: birds non-committal, headshakes_yes: headshakes happened, up: birds sitting or standing; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; 1 P: one visitor, 3 P: three visitors; L&F: loud and fast, S&S: silent and slow; pos: positive correlation; **inv:** inverse correlation; n.s.: correlation not significant; *italics:* correlation tendentially significant; coloured cells: r^2-values exceeding 10 % of explained variance; partial rank correlations: Spearman's rho.

Conspecific Presence During Human Presence	**B_1 (1 P, L&F)**	**B_2 (1 P, S&S)**	**C_1 (1 P, S&S)**	**C_2 (1 P, L&F)**	**X (3 P, S&S)**	**Y (3 PL&F)**
alert	n.s.	*pos*	pos	pos	n.s.	*pos*
rest&Co	***inv***	**inv**	**inv**	n.s.	n.s.	n.s.
headshakes_yes	n.s.	*pos*	n.s.	*pos*	pos	n.s.
up	pos	*pos*	pos	n.s.	n.s.	**inv**

With respect to the parameters 'alert' (upon occurrence: positive) and 'rest&Co' (upon occurrence: inverse), table 5.1-11 suggests the **direction** of focal-group responses to conspecific presence to remain **unchanged** during human visitation (cf. tab. 5.1-8) but the **extent** of influence to be **less than prior** to and **similar to after** visitation (excepting B_2 and C_1, both 1 P, S&S). As regards the parameters 'headshakes_yes' (positive: group X), and 'up' (inverse: Y), significant correlations were obtained for only one dataset each.

The following passages briefly list for each parameter in turn the significant results for which the amount of variance explained equalled at least 10 %; all values are provided in table 5.1-12.

Behaviour states: Conspecific presence **during** human visitation appeared to influence focal-group vigilance ('alert') only at group C (dataset C_1, 1 P, S&S, dataset C_2, 1 P, L&F), in which it explained approximately 17 % and 10 % of the variance, respectively. It had a substantial impact on behaviours subsumed in the category 'rest&Co' at dataset B_2 (1 P, S&S; approx. 33 % explained variance) and dataset C_1 (1 P, S&S; approx. 23 % explained variance), but not at the remaining datasets.

Behaviour event: Conspecific presence explained approx. 15 % of the variance **during** visitation at group X (3 P, S&S), but did not ‘cross the 10 % threshold’ in any of the other datasets.

Posture: Variation in numbers of conspecifics present **during** human visitation failed to explain postural variance (parameter ‘up’) in five of the six datasets. With respect to group Y (3 P, L&F), however, an inverse correlation accounted for approx. 28 % of the variation recorded (see tab. 5.1-12).

Table 5.1-12: Percentage of Variance in Four Parameters of Focal-Group Behaviour as Explained by Conspecific Presence during Human Visitation (with Human Visitation Partialled out). alert: birds vigilant, rest&Co: birds non-committal, headshakes_yes: headshakes happened, up: birds sitting or standing; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; 1 P: one visitor, 3 P: three visitors; L&F: loud and fast, S&S: silent and slow; dur: during human visitation; r^2: *r*-square-values (percentage of explained variance); *p*: significance (two-tailed); t: number of sampling points; n.s.: not significant; *italics*: correlation only tendentially significant; **boldface**: inverse correlation; partial rank correlations: Spearman’s rho.

	Dataset	Number of Sessions	r^2	*p*	t
Alert	B_1_1 P_L&F	8	n.s.	0.447	141
	B_2_1 P_S&S	3	*0.064*	*0.073*	53
	C_1_1 P_S&S	6	0.173	0.000	116
	C_2_1 P_L&F	3	0.104	0.023	51
	X_3 P_S&S	5	n.s.	0.849	92
	Y_3 P_L&F	5	*0.035*	*0.080*	92
Rest & Co	B_1_1 P_L&F	8	***0.024***	*0.067*	141
	B_2_1 P_S&S	3	**0.329**	0.000	53
	C_1_1 P_S&S	6	**0.233**	0.000	116
	C_2_1 P_L&F	3	n.s.	0.490	51
	X_3 P_S&S	5	n.s.	0.779	92
	Y_3 P_L&F	5	n.s.	0.674	92
Headshakes_yes	B_1_1 P_L&F	8	n.s.	0.772	135
	B_2_1 P_S&S	3	*0.057*	*0.095*	53
	C_1_1 P_S&S	6	n.s.	0.795	114
	C_2_1 P_L&F	3	*0.058*	*0.093*	51
	X_3 P_S&S	5	0.147	0.000	92
	Y_3 P_L&F	5	n.s.	0.254	92
Up	B_1_1 P_L&F	8	0.045	0.013	141
	B_2_1 P_S&S	3	*0.067*	*0.063*	53
	C_1_1 P_S&S	6	*0.026*	*0.089*	116
	C_2_1 P_L&F	3	n.s.	0.201	51
	X_3 P_S&S	5	n.s.	0.453	92
	Y_3 P_L&F	5	**0.278**	0.008	92

5.1.4.3 Impact of Human Visitation on Focal-Group Behaviour

5.1.4.3.1 Section Summary

On the focal-group level, human visitation significantly affected the parameters ‘alert’ and ‘rest&Co’ (behaviour states) in the majority of datasets examined. With respect to these parameters, the extent to which the groups responded differed substantially (s.b.). Although positive correlations were obtained in five out of six datasets, the parameters ‘headshakes_yes’ (behaviour event: max. r^2 = 9 %) and ‘up’ (aspect ‘posture’: max. r^2 = 5 %) fell short of the criterion ‘biologically meaningful’ (r^2-values = 10 %).

For the parameters ‘alert’ and ‘rest&Co’, initial exposure to the regime ‘one visitor, loud and fast’ (1 P, L&F) effected the strongest responses, followed by exposure to either of the three-visitor-regimes (for which L&F conduct resulted in minimally stronger responses than S&S conduct), and post-switch exposure to 1 P, S&S. Rank order for the remaining two datasets (C_1 and C_2, at the ‘less responsive end’ of the gradient) varied between parameters.

Following, results are presented in detail.

5.1.4.3.2 Partial Rank Correlations of Intensity of Human Impact and Focal-Group Behaviour

Eliminating the influence of conspecific presence, partial rank correlations (Spearman’s rho) were calculated for the pairs of variables listed in table 5.1-13.

Table 5.1-13: **Variables for which Partial Rank Correlations were Computed between Human Visitation and Focal-Group Behaviour (with Conspecific Presence Partialled out).** partial rank correlations: Spearman’s rho.

Variable 1 (PPIV-H)	Variable 2
human visitation	alert (behaviour state)
	rest&Co (behaviour state)
	headshakes_yes (behaviour event)
	up (posture)

Results on partial rank correlations between human visitation and the four behaviour parameters are summarised in table 5.1-14 and presented in detail in table 5.1-15.

N.b.: As introduced in chapter 4.4.2.3 and repeated in section 5.1.1, classed proportions of explained variance (r^2) and levels of significance (p) have been colour-coded (tabs. 5.1-3 and 5.1-4). Tendentially significant r^2-values are given in *italics*, and r^2-values based on inverse correlations are given in **boldface**. Non-significant values are marked as ‘n.s.’ (tab. 5.1-14; tab. 5.1-15). Significant results were considered biologically relevant, if the amount of variance explained equalled at least 10 % (in tab. 5.1-15: r^2-values = 0.100).

Table 5.1-14: Overview – Variance in Four Parameters of Focal-Group Behaviour as Explained by Human Visitation (with Conspecific Presence Partialled out). alert: birds vigilant, rest&Co: birds non-committal; headshakes_yes: headshakes happened, up: birds sitting or standing; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; 1 P: one visitor, 3 P: three visitors; L&F: loud and fast, S&S: silent and slow; pos: positive correlation; **inv:** inverse correlation; n.s.: correlation not significant; *italics:* correlation tendentially significant; coloured cells: r^2-values exceeding 10 % of explained variance; partial rank correlations: Spearman’s rho.

Human Visitor(s)	B_1 (1 P, L&F)	B_2 (1 P, S&S)	C_1 (1 P, S&S)	C_2 (1 P, L&F)	X (3 P, S&S)	Y (3 PL&F)
alert	pos	pos	pos	pos	pos	pos
rest&Co	**inv**	**inv**	**inv**	**inv**	**inv**	**inv**
headshakes_yes	pos	*pos*	pos	n.s.	pos	pos
up	pos	n.s.	pos	pos	pos	pos

Table 5.1-14 suggests human visitation to exert a distinct impact on focal-group behaviour. Correlations found as regards the parameter ‘alert’ were invariably significantly positive; they lacked ‘biological relevance’ (as defined in THIS THESIS) only with respect to datasets C_1 (1 P, S&S) and C_2 (1 P, L&F post-switch). Human visitation was invariably significantly inversely correlated with the parameter ‘rest&Co’, with an r^2-value below 10 % obtained only for dataset C_1 (1 P, S&S). As for the parameters ‘headshakes_yes’ and ‘up’, response directions were significantly positive (increase in behaviour with increase in impact of visitation as measured by the PPIV-H) in five, and non-significant in one dataset (C_2 for the former, B_2 for the latter parameters), but never attained biological relevance (as defined in THIS THESIS, i.e., correlations were statistically significant, but r^2-values below 10 %).

The following passages briefly examine the absence/ presence of response gradients by ranking the different visiting regimes according to amount of variance explained for each of the four parameters; all values are provided in table 5.1-15.

Behaviour states: Human visitation explained between approximately 7 % (dataset C_2, 1 P, L&F after initial exposure to 1 P, S&S) and approximately 34 % (dataset B_1, 1 P, L&F) of the variance in the parameter ‘alert’ (tab. 5.1.-15). Correlations were positive, i.e., increased proximity resulted in increased vigilance. The r^2-values for both datasets of group C fell short of the 10 % threshold. In decreasing order, the datasets could be arranged as follows:

$$B_1 >> Y \cong X >> B_2 > C_1 \cong C_2$$

or, in terms of regimes,

1 P, L&F >> 3 P, L&F ≅ 3 P, S&S >> 1 P, S&S (post-switch) > 1 P, S&S ≅ 1 P, L&F (post-switch)

The parameter ‘rest&Co’ was inversely affected, i.e., increased proximity led to a decrease in non-committal behaviours (tab. 5.1-15). With regard to this parameter, human visitation explained between 8 % (dataset C_1, 1 P; S&S) and approx. 32 % (dataset B_1, 1 P, L&F) of the variance. Only the r^2-values for dataset C_1 failed to exceed the 10 % threshold. In decreasing order, the datasets could be arranged as follows:

$$B_1 >> Y \cong X >> B_2 \cong C_2 > C_1$$

or, in terms of regimes,

1 P, L&F >> 3 P, L&F ≅ 3 P, S&S >> 1 P, S&S (post-switch) ≅ 1 P, L&F (post-switch) > 1 P, S&S

Behaviour event: Variations in visitor distance during human visitation were only weakly related to variations in the parameter ‘headshakes_yes’ (all r^2-values < 10 %). Between-regime differences were not readily discernible, and no gradients in line with intensity of movement were found. There was, however, a slight difference between those datasets approached by only one visitor (proportions of explained variance below 2 % or non-significant) and those visited by a ‘threesome’ (r^2-values 9 % and 7 % for groups X and Y, respectively; tab. 5.1-15).

Posture: Variations in visitor distance during human visitation were only weakly related to variations in posture (‘up’), with percentages of explained variance below 5 % for all datasets (tab. 5.1-15). With respect to the parameter ‘up’, between-regime differences were not readily discernible, and no gradients in line with intensity of movement or number of visitors were found.

Table 5.1-15: Percentage of Variance in Four Parameters of Focal-Group Behaviour as Explained by Human Visitation (with Conspecific Presence Partialled out). alert: birds vigilant, rest&Co: birds non-committal, headshakes_yes: headshakes happened, up: birds sitting or standing; B_1, C_1: datasets prior to switch in visiting regime, B_2, C_2: datasets after switch in visiting regime; 1 P: one visitor, 3 P: three visitors; L&F: loud and fast, S&S: silent and slow; r^2: *r*-square-values (percentage of explained variance); *p*: significance (two-tailed); t: number of sampling points; n.s.: not significant; *italics*: correlation only tendentially significant; **boldface**: inverse correlation; partial rank correlations: Spearman's rho.

	Dataset	Number of Sessions	r^2	*p*	t
Alert	B_1_1 P_L&F	8	0.337	0.000	466
	B_2_1 P_S&S	3	0.142	0.000	165
	C_1_1 P_S&S	6	0.085	0.000	331
	C_2_1 P_L&F	3	0.068	0.001	175
	X_3 P_S&S	5	0.245	0.000	298
	Y_3 P_L&F	5	0.253	0.000	290
Rest & Co	B_1_1 P_L&F	8	**0.322**	0.000	466
	B_2_1 P_S&S	3	**0.168**	0.000	165
	C_1_1 P_S&S	6	**0.080**	0.000	331
	C_2_1 P_L&F	3	**0.140**	0.000	175
	X_3 P_S&S	5	**0.226**	0.000	298
	Y_3 P_L&F	5	**0.235**	0.000	290
Headshakes_yes	B_1_1 P_L&F	8	0.017	0.006	452
	B_2_1 P_S&S	3	*0.019*	*0.073*	*162*
	C_1_1 P_S&S	6	0.018	0.015	322
	C_2_1 P_L&F	3	n.s.	0.174	171
	X_3 P_S&S	5	0.093	0.000	297
	Y_3 P_L&F	5	0.073	0.000	286
Up	B_1_1 P_L&F	8	0.018	0.004	466
	B_2_1 P_S&S	3	n.s.	0.204	165
	C_1_1 P_S&S	6	*0.009*	*0.085*	331
	C_2_1 P_L&F	3	0.046	0.004	175
	X_3 P_S&S	5	0.022	0.012	298
	Y_3 P_L&F	5	0.017	0.026	290

5.1.4.4 Comparison of Correlations: Responses to Conspecifics during Human Visitation vs. Responses to Human Visitation

Comparison of focal-group responses to conspecific presence during human visitation with those elicited by human visitation itself (partial rank correlations) showed **impact of human visitation to exceed impact of conspecific presence** in four out of six datasets each as regards the categories 'alert' and 'rest&Co' (tab. 5.1-16). In the remaining two datasets, focal-group responses in the category 'alert' were more strongly correlated with conspecific presence than with human visitation at group C (C_1 1 P, S&S; C_2 1 P, L&F) regardless of visiting regime, with the latter explaining less than 10 % of overall variance both times. Concerning the category 'rest&Co', responses more strongly correlated with conspecific presence were found in the regime '1 P, S&S' only (B_2, C_1): With respect to these datasets, responses to human visitation explained less than 10 % of overall variance at dataset C_1 (but not at any of the others), while dataset B_2 was the only one at which explanation of overall variance exceeded 10 % for human visitation *as well as* conspecific presence.

In the categories 'occurrence of headshakes_yes' and 'up', correlations with human visitation never exceeded the 10 % threshold. Concerning conspecific presence, they did so only once per category ('headshakes_yes': group X_{positive}; 'up': group $Y_{\textbf{inverse}}$). Except for these two, no clear 'preferences' could be discerned.

Table 5.1-16: Comparison of Correlations between Focal-Group Response and Conspecific Presence Found during Human Visitation to Correlations between Focal-Group Response and Human Visitation. Correlations are compared with respect to strength of correlation (r^2-value) and number of biologically relevant ($r^2 = 10$ %) significant correlations obtained for each of four parameters. alert: birds vigilant, rest&Co: birds 'non-committal', headshakes_yes: headshakes happened, up: birds sitting or standing; B_1, C_1: datasets pre-switch, B_2, C_2: datasets post-switch (in visiting regime); 1 P: one visitor, 3 P: three visitors; L&F: loud and fast, S&S: silent and slow; allD: all datasets (sum of biologically relevant correlations); H_: human visitation, C_: conspecific presence (during human visitation); r^2: r-square-values (% of explained variance); p/ sig: significance (two-tailed); *: correlation significant at $p < 0.05$; **: correlation significant at $p < 0.01$; correlation significant at $p < 0.001$; *italics*$^{(*)}$/ tend: correlation only tendentially significant ($0.05 < p < 0.1$), n.s.: not significant, **boldface**: inverse correlation; partial rank correlations: Spearman's rho. Rose and pink colouration according to strength of relationship (r^2-values); grey: conspecific presence vs. human visitation summed up across all r^2-values regardless of significance level; dark orange: both correlations significant, pale orange: one correlation significant, white: correlation at best tendentially significant. **N.b.:** Similar or identical r^2-values for conspecific presence and human visitation were never obtained.

Behaviour Parameter	Dataset and Visiting Regime	r^2-values		dataset	r^2 C_ > r^2 H_				r^2 C_ < r^2 H_		
		r^2 C_	r^2 H_		r^2 C_ greater r^2 H_	r^2 C_sig & r^2 H_sig	r^2 C_tend & r^2 H_tend	r^2 C_tend & r^2 H_n.s.	r^2 C_ smaller r^2 H_	r^2 C_tend & r^2 H_sig	r^2 C_n.s. & r^2 H_sig
Alert	B_1 1P, L&F	n.s.	0.337***	B_1					x		1
	B_2 1P, S&S	*0.064*$^{(*)}$	0.142***	B_2					x	1	
	C_1 1P, S&S	0.173***	0.085***	C_1	x	1					
	C_2 1P, L&F	0.104*	0.068**	C_2	x	1					
	X 3P, S&S	n.s.	0.245***	X					x		1
	Y 3P, L&F	*0.035*$^{(*)}$	0.253***	Y					x	1	
	allD $r^2 \geq 10\%$	2	4	allD	2	2	0	0	4	2	2
Rest&Co	B_1 1P, L&F	***0.024***$^{(*)}$	**0.322*** **	B_1					**x**	**1**	
	B_2 1P, S&S	**0.329*** **	**0.168*** **	B_2	**x**	**1**					
	C_1 1P, S&S	**0.233*** **	**0.080*** **	C_1	**x**	**1**					
	C_2 1P, L&F	n.s.	**0.140*** **	C_2					**x**		**1**
	X 3P, S&S	n.s.	**0.226*** **	X					**x**		**1**
	Y 3P, L&F	n.s.	**0.235*** **	Y					**x**		**1**
	allD $r^2 \geq 10\%$	2	5	allD	2	**2**	0	0	**4**	**1**	**3**
Headshakes_yes	B_1 1P, L&F	n.s.	0.017**	B_1					x		1
	B_2 1P, S&S	*0.057*$^{(*)}$	*0.019*$^{(*)}$	B_2	x		1				
	C_1 1P, S&S	n.s.	0.018*	C_1					x		1
	C_2 1P, L&F	*0.058*$^{(*)}$	n.s.	C_2	x			1			
	X 3P, S&S	0.147***	0.093***	X	x	1					
	Y 3P, L&F	n.s.	0.073***	Y					x		1
	allD $r^2 \geq 10\%$	1	0	allD	3	1	1	1	3	0	3
Up	B_1 1P, L&F	0.045*	0.018**	B_1	x	1					
	B_2 1P, S&S	*0.067*$^{(*)}$	n.s.	B_2	x			1			
	C_1 1P, S&S	*0.026*$^{(*)}$	*0.009*$^{(*)}$	C_1	x		1				
	C_2 1P, L&F	n.s.	0.046**	C_2					x		1
	X 3P, S&S	n.s.	0.022*	X					x		1
	Y 3P, L&F	**0.278** **	0.017*	Y	**x**	**1**					
	allD $r^2 \geq 10\%$	1	0	allD	4	2	1	1	2	0	2
Sum	$B_1 r^2 \geq 10\%$	0	2	B_1	1	1	0	0	3	1	2
	$B_2 r^2 \geq 10\%$	1	2	B_2	3	1	1	1	1	1	0
	$C_1 r^2 \geq 10\%$	2	0	C_1	3	2	1	0	1	0	1
	$C_2 r^2 \geq 10\%$	1	1	C_2	2	1	0	1	2	0	2
	$X r^2 \geq 10\%$	1	2	X	1	1	0	0	3	0	3
	$Y r^2 \geq 10\%$	1	2	Y	1	1	0	0	3	1	2
	allD $r^2 \geq 10\%$	6	9	allD	11	7	2	2	13	3	10

In general, there was **little evidence of a complementary relationship** of the two types of disturbances (conspecifics vs. humans). A comparison of tables 5.1-12 and 5.1-15 shows only three cases for the regime ‘1 P, S&S’ (i.e., ‘alert’: C_1; ‘rest&Co’: B_2, C_1), in which weak responses to human visitation were complemented by pronounced responses to conspecific presence. On the level of focal-group evaluations, findings thus suggested **conspecific** presence to constitute a **‘background noise’** on top of which **human visitation** exerted an **additional impact** which clearly exceeded that of conspecifics in all but the ‘mildest’ of visiting regimes.

5.1.5 Focal Groups – Chapter Summary

Even though more pronounced responses had frequently been observed from 1st-row birds, Friedman-test found ***between-row differences*** to be statistically not significant.

Predominant behaviour categories did not differ among datasets: In *all rows* and **all periods**, the categories ‘alert’ and/or ‘rest&Co’ for the aspect ‘behaviour states’, ‘occurrence of headshakes_none’ (aspect ‘behaviour event’), and ‘prone’ (aspect ‘posture’) were predominant. Moreover, with respect to the aspect ‘behaviour states’, little overall change was found in the remaining categories[21] .

Between-period differences in the categories ‘alert’, ‘rest&Co’, ‘occurrence of headshakes_yes’ and ‘up’ were found in **all datasets**. Median index-values **during** visitation increased distinctly for the category ‘alert’, and slightly for the categories ‘occurrence of headshakes_yes’ and ‘up’. They decreased distinctly for the category ‘rest&Co’. This trend was reversed **after** visitation.

Between-group differences **prior** to visitation were pronounced for the categories ‘alert’ and ‘rest&Co’, but mostly small for the categories ‘occurrence of headshakes_yes’ and ‘up’. The former were therefore assessed by looking at the magnitude of increase/ decrease in index-values, rather than by examination of absolute differences.

Between-regime differences **during** and **after visitation** indicated that for the categories ‘alert’ and ‘rest&Co’ (aspect ‘behaviour states’) loud and fast visitation elicited a more pronounced response than silent and slow visitation. In contrast, the number of visitors appeared to be of relevance only within the silent and slow regimes. With respect to the categories ‘occurrence of headshakes_yes’ and ‘up’, between-regime differences were not readily discernible, and no gradients in line with intensity of movement were found for either. Concerning the parameter ‘headshakes_yes’, three visitors elicited slightly more pronounced responses than a single visitor.

Impact of conspecific presence **prior to** and **after** human visitation was not directly related to absolute (PPIV-C) or proportional numbers (i.e., relativised by focal-group size; see fig. 5.1-23 b) of conspecifics observed, in that focal-group responses neither consistently increased nor decreased with increasing numbers of conspecifics for any of the parameters examined. Within each dataset, r^2-values explaining more than 10 % of the variance were found *either* prior to *or* after human visitation for each of the parameters analysed. **Prior to** visitation, responses of group X (3 P, S&S) were most strongly (of all datasets) correlated with conspecific presence for all four parameters. **After** visitation, maximum correlations were lower and spread across datasets. The extent of existent correlations nevertheless suggested that potential conspecific influence be kept in mind during visitation.

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[21] and these were not included in correlation analyses

Correlations between focal-group response and conspecific presence **during** human visitation (partial rank correlations) were generally weaker than those found **prior to** visitation (seven cases, including three only tendentially significant ones) or entirely failed to attain statistical significance (ten cases, incl. two for which pre-visit values had also been n.s.; cf. tabs. 5.1-9 and 5.1-12). 'Stronger' correlations during- than pre-visitation were encountered less often and mostly when no correlation (n.s.) had been found before visitation (five out of a total of seven cases). Moreover, in the categories 'alert' and 'rest&Co', correlations during visitation exceeded those prior to visitation for the regime '1 P, S&S' (B_2, C_1) only. No such clear pattern emerged when during-visit correlations were compared to **post-visit** correlations (cf. tabs. 5.1-9 and 5.1-12).

Comparison of focal-group responses to ***conspecific presence*** during human visitation with those elicited by ***human visitation*** itself showed impact of human visitation to exceed impact of conspecific presence in four out of six datasets each as regards the categories 'alert' and 'rest&Co' (tab. 5.1-16).

Owing to generally less pronounced responses in the categories 'occurrence of headshakes_yes' and 'up', (human visitation: never above 10 %; conspecific presence: once per parameter), focal-group evaluations did not discern any clear differences in impact as regards these parameters.

Focal-group evaluations did **not** find a **complementary** impact for human visitation and conspecific presence, **but** suggested conspecific presence to constitute a non-negligible 'background noise' on top of which human visitation exerted an **additional** impact, which clearly exceeded that of conspecifics in all but the 'mildest' of visiting regimes.

5.2 Responses of Focal Animals to Disturbance: Selected Behaviour Elements and Heart Rate

> “Life is what happens while you’re busy doing something completely different.” (Lennon 1980)

Some results on rates of behaviour elements (vigilance, agonistic elements) and their relation with heart rate and disturbance were published prior to completion of this thesis (Schuster 2008; appendix 5.2-1). Rather than repeatedly referring to the paper, the gist of the findings is briefly summarised in the following section.

5.2.1 Database

Focal-Animal Behaviour Element Analyses were based on data from a total of 23 penguins in 5 groups (4-5 birds per study group). Data from 16 focal animals in 5 groups were also used in **Focal-Animal Heart Rate Analyses**. Tab. 5.2-1 provides results on those 16 birds for which simultaneous records could be analysed. Numbers of incubating birds were complemented by a fluctuating number of **conspecifics**.

5.2.2 Analyses

Rank correlations (Spearman’s rho) were based on 20 s-interval values of behaviour, heart rate, and disturbance (the latter expressed as Interval Performance Indicator Values: IPIV-C, IPIV-H; q.v.); vigilance and agonistic behaviour elements were analysed as proportions of behaviour displayed per 20 s-interval, and HR was analysed as beats per minute values (bpm) extrapolated from 20 s-intervals.

5.2.3 Summary of Results

While **agonistic** behaviour elements were more often recorded in response to conspecific disturbance, **heart rate** and **vigilance** corresponded more closely to human disturbance (tab. 5.2-1).

Heart rate responses of the majority of the 16 focal penguins did not correlate (n = 8) or were inversely (n = 3) correlated with conspecific disturbance with respect to both total disturbance and disturbance at the nest (max. positive r^2: 0.05 for total disturbance, 0.06 for disturbance at the nest; tab. 5.2-1). In contrast, heart rate of nine of the 12 birds that were subjected to human visits was significantly correlated with human disturbance (max. $r^2 = 0.13$; tab. 5.2-1), whereas for one penguin (FA-B3-1), the correlation was inverse ($r^2 = 0.07$; tab. 5.2-1), and no statistically significant correlation was found for the remaining two focal birds.

Vigilance of 13 of 16 focal animals showed a significant positive correlation with total conspecific disturbance (max. $r^2 = 0.26$) and with conspecific disturbance at the nest (max. $r^2 = 0.16$). Nine of 12 focal birds (the other FAs pertained to group A which did not receive any visits) significantly positively responded to human disturbance (max. $r^2_{pos} = 0.31$) with increased vigilance (tab. 5.2-1).

Agonistic elements were significantly positively correlated with conspecific disturbance in all focal animals (max. $r^2 = 0.64$) with respect to both total disturbance and disturbance at the nest (single exception: A6-2, no correlation for conspecific disturbance at the nest). They were found to be unrepresentative as ‘universal’ indicators of human disturbance, since only six of 12 birds exhibited these responses (max. $r^2 = 0.27$; tab. 5.2-1).

Table 5.2-1: Correlations of Vigilance, Agonistic Behaviour, and Heart Rate with Conspecific and Human Disturbance. Entries display r^2-values and statistical significances (p) for responses in heart rate (HR), vigilance (V), and agonistic behaviour (A) to total conspecific disturbance (C_tot Dist.), conspecific disturbance at the focal nest (C_a Dist.), and total human disturbance (H Dist.). Additionally, the relationship between heart rate and vigilance is shown (HR x V). FA: focal animal; FAs identified by alphanumerical code. Visiting regimes: FAs-A: unvisited; FAs-B: 1 P, L&F; FAs-C: 1 P, S&S; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; S&S: silent and slow, L&F: loud and fast; 1 P: one visitor, 3 P: three visitors. Rank correlations (Spearman's rho) based on 20 s-interval values. Disturbance types analysed as Interval Performance Indicator Values (IPIV-C, IPIV-H; q.v.); vigilance and agonistic behaviour elements analysed as proportions, HR analysed as beats per minute values (bpm). Significance levels (two-tailed) of correlations represented by asterisks: *$p<0.05$, **$p<0.01$, ***$p<0.001$, n.s.: not significant, n.a.: not applicable (e.g., at FAs-A, no visitation). **Boldface** signifies inverse correlations. t (sampling points per penguin and parameter): 54-1053 (median: 280).

			Regime															
			Never Visited				**1 P, L&F**				**1 P, S&S**			**3 P, S&S**			**3 P, L&F**	
Parameter		**FA**	A5-1	A5-2	A6-1	A6-2	B3-1	B3-2	B4-1	B4-2	C1-1	C11-1	C2-2	X1-1	X2-1	X2-2	Y5-1	Y5-2
C_tot Dist.	**HR**	r^2	**0.14**	0.01	0.00	0.02	**0.01**	0.02	0.00	0.01	0.01	**0.04**	0.00	0.02	0.05	**0.07**	0.01	0.04
		p	***	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	*	n.s.	**	***	***	*	*
	V	r^2	0.05	0.00	0.09	**0.00**	0.04	0.08	0.04	0.03	0.05	0.13	0.09	0.26	0.08	0.06	0.09	0.02
		p	***	n.s.	***	n.s.	***	***	**	**	**	***	***	***	***	***	***	n.s.
	A	r^2	0.06	0.16	0.64	0.17	0.16	0.06	0.10	0.05	0.19	0.06	0.16	0.21	0.22	0.10	0.09	0.11
		p	***	***	***	***	***	***	***	***	***	**	***	***	***	***	***	***
C_a Dist.	**HR**	r^2	**0.00**	0.00	0.02	n.a.	**0.01**	0.00	0.01	0.01	0.02	**0.01**	0.00	0.01	0.06	**0.02**	0.02	0.01
		p	n.s.	n.s.	n.s.	n.a.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	***	*	***	n.s.
	V	r^2	0.01	0.00	0.02	0.00	0.05	0.05	0.07	0.03	0.06	0.06	0.03	0.16	0.08	0.10	0.01	0.03
		p	*	n.s.	*	n.s.	***	***	***	**	**	**	***	***	***	***	*	n.s.
	A	r^2	0.10	0.08	0.28	**0.00**	0.34	0.43	0.17	0.12	0.10	0.04	0.10	0.28	0.37	0.18	0.02	0.31
		p	***	***	***	n.s.	***	***	***	***	***	*	***	***	***	***	***	***
H Dist.	**HR**	r^2	n.a.	n.a.	n.a.	n.a.	**0.07**	0.03	0.11	0.03	0.13	0.11	0.04	0.00	0.04	0.08	0.04	0.00
		p	n.a.	n.a.	n.a.	n.a.	***	**	***	*	***	***	***	n.s.	***	***	***	n.s.
	V	r^2	n.a.	n.a.	n.a.	n.a.	0.01	0.11	0.23	0.31	0.00	0.16	0.02	0.05	0.10	**0.00**	0.10	0.21
		p	n.a.	n.a.	n.a.	n.a.	n.s.	***	***	***	n.s.	***	***	***	***	n.s.	***	***
	A	r^2	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.27	0.08	0.05	n.a.	0.08	0.02	n.a.	n.a.	n.a.	0.17
		p	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	***	***	**	n.a.	***	***	n.a.	n.a.	n.a.	***
Corr. HR x V		r^2	**0.02**	**0.00**	0.09	0.01	0.00	0.02	0.03	0.05	0.02	0.08	0.00	0.11	0.03	**0.00**	0.07	0.00
		p	**	n.s.	**	n.s.	n.s.	*	n.s.	*	n.s.	**	n.s.	***	***	n.s.	***	n.s.

Between **heart rate and vigilance** behaviour, a significantly positive correlation was found in seven of the 16 focal birds (max. $r^2 = 0.11$; tab. 5.2-1), in one bird these parameters were inversely correlated, and in half of the birds studied, they did not correlate at all.

These results emphasise **inter-individual differences** in intensity of response for both behaviour and heart rate. Additionally, they suggest different response 'preferences' with respect to different behaviour systems (vigilance, agonistics) as well as behaviour vs. heart rate. While caution is needed interpreting agonistic response intensities (as these might in part be due to differential exposure of different FAs to conspecific presence/ action), sex differences (with males being more aggressive) might appear the most parsimonious explanation for the majority of consistent differences found as regards responses of FAs from the same focal nest towards conspecifics at the nest as well as towards humans (but see Discussion).

N.b.: To avoid unnecessary lengthening of the text, the term **'comportment'** is used to jointly refer to focal-animal behaviour, posture, and heart rate.

5.3 Responses of Focal Animals to Disturbance: Behavioural, Postural and Heart Rate Topography

Following evaluations of focal-group behaviour (see chapter 5.1) and focal-animal behavioural elements (see summary 5.2), the **'flow'** of behaviour systems, postures, and heart rate before, during and after disturbance was assessed to examine changes in overall performance of individual birds.

Recapitulation: In this context, **'flow'** combines the **overall prevalence** of behaviours belonging to a given **behaviour system** with the duration of **phases** found within that system as well as capturing **changes** between different behaviour systems (e.g., comfort 2 min, vigilance 20 s, comfort 10 s, vigilance 5 s) and 'smoothness' of **transitions** between systems (e.g., instant switches between systems, interruptions of one system by elements pertaining to another system, transitionary phases comprising elements of two different systems).

Taken together, these are referred to as the animal's **behavioural topography**, and visualised as follows: Behaviour systems are coded numerically, with numbers attempting to reflect differences in focus and intensity (from resting to offensive agonistics). If plotted against time, each behaviour system is thus represented by a straight line on a system-specific horizon (analogous to horizons of a geographical landscape), while changes are indicated by the line 'jumping' from one horizon to the next.

Focal-animal comportment differed markedly across sessions within a given FA, and among different focal animals observed on the same day and at the same location. Therefore, no attempt was undertaken to average same-FA or same-day data prior to pooling. Databases for results are provided in each section. For presentation of results, focal animals visited under the same regime are pooled to examine whether the sum and range of individual reactions to the same visiting regime permitted a deeper insight into gradation of responses to different degrees of disturbance.

N.b.: As mentioned in chapter 4, evaluations of focal-animal comportment had to be entirely discarded with respect to dataset B_2 (1 P, S&S, after switch in visiting regime). As for dataset C_2 (1 P, L&F, post-switch), three sessions recorded on the first day after the switch in regime were available. Since these did not show any striking differences in response (as compared to sessions conducted under the regime 1 P, S&S), however, they were not evaluated separately, but are treated together with C_1, resulting in that conglomerate of FAs being denoted as FAs-$C_{1,2}$.

In the following sections (text, tabulated results), focal animals are specified by the group[1] they belonged to (e.g., FAs-X), which for groups X (3 P, S&S) and Y (3 P, L&F) automatically determines the visiting regime (no switch). For focal animals pertaining to groups B and C, respectively, specification of the dataset is additionally provided (FAs-B_1: 1 P, L&F), FAs-$C_{1,2}$: 1 P, S&S, and 3 sessions of the first day post-switch, viz., 1 P, L&F).

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[1] group designations being shorter than regime designations

Behavioural, postural, and heart rate **topography** were examined on **three levels**:

1. **Visual Appraisal** comprised a qualitative, 'graphical' examination of changes in comportment before, during, and after human visitation as well as changes in response to conspecific, and predator/ aircraft disturbance. Following this, the question of consistency of these changes across focal animals was addressed quantitatively (key question: 'How many?').

   Questions as to magnitude and structure of these changes which arose from visual appraisal were then addressed in the following sections.
2. **Quantitative Comparison of Prevalence** of behaviour systems and postures examined changes in proportional occurrence of each parameter before, during, and after human visitation. This was complemented by analyses of heart rate variation using a set of 8 (descriptive) statistical parameters (key question: 'How much?').
3. **Distribution of Phase/ State Durations** of behaviour phases, posture states and heart rate phases before, during, and after human visitation examined alterations in 'flow', by quantifying changes in the duration of phases and states (key question: 'In what way?').

5.3.1 Visual Appraisal of Changes in Comportment

Visual appraisal comprised the following steps:

1. Coded information on focal-animal comportment and disturbance was entered in two separate spreadsheets (see topography-chart-files in appendix 5.3.1-1).
   a. Focal-animal behaviour systems and postures were assigned to topographical classes (tab. 5.3.1-2) which captured changes in focus and/ or intensity of the respective behaviours. Focal-animal heart rate was entered as 20 s-counts (not bpm!).
   b. Disturbance parameters comprised human, conspecific, and predator/ aircraft disturbance.
2. Charts (see fig. 5.3.1-2) were created to visually align the topography of focal-animal comportment with disturbance parameters (humans, conspecifics, predator/ aircraft).
3. These topography charts were used to systematically appraise for each session
   a. focal-animal comportment pre-visitation ('baseline'),
   b. changes in focal-animal comportment during human visitation,
   c. changes in focal-animal comportment after visitation, and
   d. changes in focal-animal comportment in conjunction with changes in conspecific presence and movement, presence of predators, and aircraft noise.
4. The results obtained per session were pooled for all focal animals (FAs-allReg) as well as by visiting regime (e.g., FAs-X); and between period differences as well as between-regime differences for each behaviour system, postures, and heart rate were examined.

For visual appraisal, 51 sessions (from 19 FAs) in the course of which human visitation had taken place constituted the database (tab. 5.3.1-1).

Table 5.3.1-1: Database used for Visual Appraisal. FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

	FAs-allReg	FAs-B_1	FAs-$C_{1,2}$	FAs-X	FAs-Y
Number of Sessions	51	17	16	12	6
Number of Focal Animals	19	5	5	5	4

5.3.1.1 Methodological Prelude

Recapitulation: Primary transcriptions had served to unite information collected by various media (video, data logger, field notebook) in hard-copy transcription matrices (paper). They had yielded a second-by-second account of focal animal behaviour elements and posture, conspecific presence and actions, as well as human visitation. The paper sheet also contained times of ad lib. sightings of predators or (auditory perception of) aircraft. With respect to focal-animal heart rate, logger data (voltage files) had been transformed into counts of heartbeats per 20 s-interval and the resulting figures added to the matrix (every 20th second).

5.3.1.1.1 Secondary Transcription of Focal-Animal Comportment and Disturbance

Secondary transcriptions focused on duration and distribution of each of the behaviour systems, both postures, and heart rate in relation to the different types of disturbance (visiting regimes, conspecifics, to a lesser extent predators/ aircraft).

■ Creation of Spreadsheets and Topography Charts

For each session, **two** separate Excel **spreadsheets** contained data on focal-animal comportment and disturbance, respectively. Three graphs (à 10 min) were created per spreadsheet. The resulting set of six graphs constituted the **topography chart** of that session.

Focal-animal comportment: Focal-animal behaviour systems were assigned to **topographical classes** (tab. 5.3.1-2), and the respective code-values were entered into the first spreadheet (second-by-second).

The code employed reflects the attempt to capture changes in focus and increasing intensity of behaviours (from ‘unfocused and ‘noncommittal’ = rest = class 1, to ‘focus on outward, likely threatening events’ = offensive agonistics = class 7). **Exceptions** were made with respect to certain behaviours for which previous studies had occasionally or repeatedly reported a connection with human disturbance, viz., shakes and displays. These were taken out of their behaviour systems (comfort and breeding, resp.), and assigned to a separate class (class 4): Within the behaviour system of comfort (remaining behaviours: class 2), the ‘ambiguous’ nature of ruffle-shakes and particularly headshakes (e.g., Ainley 1974, Frings & Frings 1959, Schmidt-Nielson & al. 1958) as elements of both comfort and possible indicators of disturbance, was thus emphasised. Since early accounts of pygoscelid penguin behaviour (e.g., Bagshawe 1938, Levick 1907) had reported display actions to increase during or immediately after disturbance (e.g., humans walking through a colony), ecstatic and mutual displays likewise received a value distinct from that of other breeding behaviours (which were subsumed in class 3). Given the rarity of these within the data set, however, shakes and displays were assigned to the same category. Distinction between the former and the latter was unequivocal, as shakes never lasted longer than 1-3 s, whereas displays invariably took longer than that. If these behaviours occurred together with other behaviours within the same second (seconds-at-two-systems, q.v.), they were given prominence.

To clearly set off vigilance (class 6) and agonistic behaviours (class 7), a **‘gap’** (GAP 1 in tab. 5.3.1-2) was inserted between these and the remaining behaviour systems (class 5 = unoccupied).

Table 5.3.1-2: Topographical Classes Attempting to Capture Changes in Focus and Intensity of Behaviour Exhibited. Shakes and displays were assigned to a separate class to examine literature-reported sensitivity to disturbance. Determination of moderate/ intense vigilance depended on durations of individual head turns/ scans and time between successive head turns/ scans; BTA: bill-to-axilla, SST: sideways stare, AST: alternate stare, P: point, G: gape; n.a.: not applicable.

Behaviour System/ Posture	Topographical Class	Focus (of FA)/ Intensity (of Behaviour)
Rest: rest/ inactive	1	'unfocused' or noncommittal
Comfort: e.g., preen, stretch, yawn (excl. headshakes)	2	self-focused
Breed: egg and nest manipulation (excl. displays)	3	focused on immediate extension of self
Separate: shakes and displays	4	frequently reported as disturbance indicators
GAP 1	5	n.a., introduced to set off vigilance and agonistics
Vigilance: moderate; intense; vigilance during wing-flaps	6	increasingly focused on outward, potentially threatening events
Agonistics: defensive (BTA; SST; AST); offensive (P; G)	7	focused on outward events perceived as: likely threatening, actually and immediately threatening
GAP 2	8-10	n.a., introduced to set off posture
Posture: prone	11	n.a., dependent on behaviour system
Posture: up	12	n.a., dependent on behaviour system

With respect to instances of **seconds-at-two-systems** (excl. shakes and displays), the class-value of the first half second was noted if behaviours could not ‘coexist’ but had to be **performed in sequence** (e.g., bill-tremors and nest manipulation; bill-shakes and agonistics; egg manipulation and preening; vigilance and agonistics; preening and vigilance; two mutually exclusive intentional behaviours). Intentional behaviours performed in the same second as ‘fully expressed’ behaviours were ignored.

Concerning behavioural elements that could be **performed simultaneously** (e.g., shuffles and yawns, backward flipper stretches and vigilance head turns), behaviours involving the head were considered more important regardless of the within-second position.

Examples: While nest-scratching can be clearly classified as breeding behaviour, shuffling (rocking on the nest) occurs both in the context of comfort and breeding behaviour. Both behaviours leave the bird free to move the head, and may accompany other behaviours such as vigilance. On their own, shuffles as well as nest-scratching behaviour were assigned to the behaviour system of breeding, but in conjunction with behaviours involving the head[2], they were ignored. Similarly, stretching movements, i.e., backward-/ forward-flipper-stretches, and yawns were assigned to comfort if they occurred without any competing behaviour and ignored if a more intense behaviour (e.g., vigilance) was expressed at the same time.

Focal-animal posture was noted as either ‘prone’ (class 11) or ‘up’ (class 12, comprising sitting and standing), and appeared as an accompanying line of dots in the same figure. Note that a larger **‘gap’** (GAP 2 in tab. 5.3.1-2) was inserted to help distinguish information on posture from data on behaviour systems.

Representation of focal-animal heart rate as a succession of unconnected black dots depicted number of heartbeats per 20s.

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[2] Shuffles in conjunction with the comfort behaviour Yawn were thus assigned to comfort.

The **second Excel spreadsheet** contained information on human and conspecific disturbance. While human disturbance was represented by the Visiting Stage Performance Indicator Value (q.v.), conspecific disturbance included ‘stationary’ presence immediately next to the focal nest (nest distance a[3], summed up for 10 s) as well as movement in three zone of increasing distance from the focal nest (separately summed up for 10 s for each distance; fig. 5.3.1-1). In addition to that, the rare recordings of skua[4] presence on the ground, skua low overflights or aircraft noise were also noted in this table.

Each of the spreadsheets was split into three 10 min-sections so that the graphs created served to represent time before, during, and after human visitation (306 graphs in total). In the order given below, the chart (comprising a ‘set’ of six graphs per session) thus depicted

1a) Focal-animal behaviour, posture, and heart rate before human visitation,
1b) Conspecific ‘disturbance’ before human visitation,
2a) Focal-animal behaviour, posture, and heart rate during human visitation,
2b) Conspecific ‘disturbance’ during human visitation,
3a) Focal-animal behaviour, posture, and heart rate after human visitation,
3b) Conspecific ‘disturbance’ after human visitation.

All charts created from these spreadsheets are found in appendix 5.3.1-1. An **exemplary charts** is shown below. For each set of parameters (behaviour/ posture; heart rate; conspecific disturbance; human disturbance), the scale (Y-axis) is generally kept constant across sessions to facilitate visual comparison; attention is drawn to changes in scale necessitated by outliers.

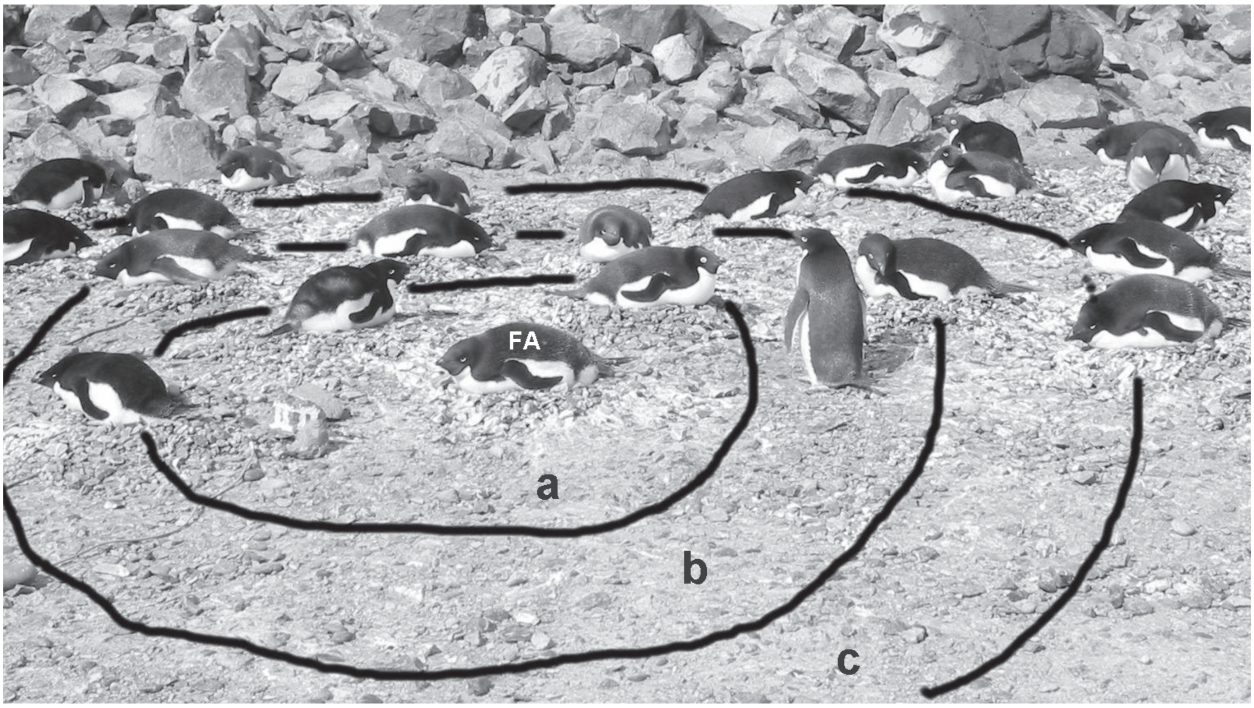

Figure 5.3.1-1: Recapitulation: Nest of a Focal Animal with Surrounding Nest Zones. Information on conspecific disturbance was evaluated by noting the birds’ presence and selected aspects of their behaviour in three zones (a, b, c) of increasing distance from the focal animal (FA). © Schuster 2006

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[3] Preliminary evaluations had shown that conspecifics standing in nest distances b, and c, did not exert any influence on focal-animal comportment.

[4] As mentioned earlier, Southern giant petrels (*Macronectes giganteus*) were neither observed on the ground nor performing low overflights in any of the sessions recorded.

■ Definitions Used To Appraise Comportment

Definitions for the appraisal parameters employed are presented in box 5.3.1-1.

Box 5.3.1-1: Definitions used To Appraise Behaviour/ Posture and Heart Rate.

'Scattering': Behaviour was defined as being 'scattered' if the bird exhibited very short periods of one behaviour system alternating with very short periods of one or more different behaviour systems. Thus, behaviour would be classified as 'scattered' either because the bird alternated rapidly between, e.g., vigilance and breeding behaviour or because elements from several behaviour systems (e.g., vigilance, rest, comfort) were shown in short succession.

'Predominant – yes': The respective behaviour system was exhibited (almost) exclusively.

'Occurs – yes': The respective behaviour system was exhibited briefly to quite commonly.

'Occurs – no': The respective behaviour system was not exhibited at all.

'Heart rate undulates regularly': Using 20 s-counts, focal-animal heart rate was found to 'undulate' more or less regularly, in that values from successive counts would often differ by one or two beats without, however, resulting in a trend (increase/ decrease). These 'undulations' were considered 'physiologically normal'.

'Behaviour Increases/ Decreases': For the focal animal, pre-visit behaviour constituted the 'baseline' for comparisons. Zero values thus indicate 'no change', rather than the non-existence of the respective behaviour. It should be noted that these terms state the occurrence of an increase/ decrease (changes in within-parameter intensity, qualitative), but do not convey any information on its magnitude (measured difference, quantitative).

'Heart Rate Increases/ Decreases': Increases/ decreases clearly broke the pattern of undulation in any of the three periods.

■ Visiting Stage Performance Indicator Value (VS-PIV) for Human Disturbance

Extent of human disturbance was expressed by the Visiting Stage Performance Indicator Value, an unweighted measure (visitor number and conduct not included, but noted in charts) which coded for approaches towards the focal-animal nest as well as movement/ presence at specific distances from the focal-animal nest; visiting stages and their respective performance indicator values are shown in table 5.3.1-3.

Table 5.3.1-3: Stages of Human Visitation as Coded by the Visiting Stage Performance Indicator Value (VS-PIV). Note that this Performance Indicator Value does not specify visitor number and conduct; information relating to these parameters is provided in the graph titles.

Visiting Stage and Distance	VS-PIV
Absence of human visitor(s)	0
Visitor(s) along colony at distance 20-25 m	13
Visitor(s) retreat	14
Visitor(s) approach to 15 m	15
Visitor(s) remain at 15 m	16
Visitor(s) approach to 5 m	17
Visitor(s) remain at 5 m	18
Visitor(s) approach to 3 m	19
Visitor(s) remain at 3 m	20

■ Conspecific Movement Measure (CMM)

The Conspecific Movement Measure (CMM) served to assess intensity and continuity of conspecific movement **prior to human visitation** for each session. For this, the five 2 min-intervals (each comprising twelve counting-intervals of 10 s) were examined and assessed according to the code presented in table 5.3.1-4. For tabulated presentation of results, the categories were pooled (none to low vs. intermediate vs. high). Note that the counting-intervals served to define whether conspecific movement was classified as being ‘intermittent’ or ‘constant’, i.e., classification was based on presence or absence of spaces between ‘blocks of summed-up conspecifics’.

Table 5.3.1-4: Conspecific Movement Measure (CMM). Within each 2 min-interval before human visitation, maximum number of conspecifics counted (per 10 s) was used for classification. Intermittent: clearly separable stretches of conspecific movement/ no conspecific movement detectable.

Pooled CMM Classes	Code	Conspecific Movement (per 10 s-Count as Seen in Topography Charts)
none to low	0	no conspecific movement at all
	0	intermittent movement of less than 5 conspecifics
	1	constant movement of less than 5 conspecifics
	1	single occurrences of movement of not more than 10 conspecifics
intermediate	2	intermittent movement of 5 to 15 conspecifics
	3	constant movement of 5 to 15 conspecifics
high	4	intermittent movement of more than 15 conspecifics
	5	constant movement of more than 15 conspecifics

■ Predator/ Aircraft Disturbance

Occurrence and duration of disturbance by predators/ aircraft was entered into matrices/ charts upon appearance.

■ Appraisal Procedure and Assessment Parameters Used

Before as well as **after** human **visitation**, visual appraisal (tab. 5.3.1-5) was undertaken for **five 2 min-intervals**. Besides setting the ‘baseline of comportment’ before and providing information on ‘post-stimulus-effects’ (persistence of reaction after the disappearance of the stimulus) after human visitation, these periods were also used for the appraisal of focal animal reactions to conspecific disturbance: Conspecific ‘stationary’ presence and movement were examined upon occurrence (empirically), and only consistent[5] responses were considered.

In order to gauge the amount conspecific disturbance the focal animals had (already) been subjected to before human visitation set in, conspecific disturbance **prior to human visitation** was additionally examined (five 2 min-intervals, s.a.) using the Conspecific Movement Measure (CMM, s.a.).

Disturbance by skua (presence on the ground/ low overflights) and aircraft (noise) was included in the appraisal, but occurrences were too infrequent to permit general comparison (and these parameters have thus been excluded from tab. 5.3.1-5).

During human visitation, focal-animal behaviour, posture and heart rate were appraised separately for **each stage of the visit** (e.g., visitor approach to 15 m, visitor at 15 m, visitor approach to 5 m, etc., VS-PIV; q.v.). Unlike during focal-group evaluations (q.v.), separating the stages of ‘approach to a certain distance’ from those of ‘stay at that distance’ was possible during visual appraisal,

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[5] inconsistent: e.g., two responses in six encounters

because of the different sampling methods employed (FG: Instantaneous-Scan Sampling vs. Continuous Recording). As the approaches had invariably taken up considerably less time than that spent at the respective distances, however, this resulted in grossly unequal time intervals which need to be taken into account with respect to the 'amount of behaviour' a bird was able to display.

Table 5.3.1-5: Assessment Parameters Used for Visual Appraisal. Appraisal comprised the establishment of 'relative baselines' prior to human visitation/ prior to human visitation and outside conspecific presence, followed by comparative assessment of focal-animal responses during and after human visitation/ during conspecific presence outside human visitation. Conspec.: conspecific; ints: intervals

Assessment Parameter	**Before Human Visitation (five 2 min-ints)**	**During (per visiting stage) and After (five 2 min-ints) Human Visitation**	**During Conspec. 'Stationary' Presence/ Conspec. Movement (pre-/ post-visitation)**
overall behaviour 'scatters'	yes (1)/ no (0)	more (1)/ less (-1)/ same (0)	more (1)/ less (-1)/ same (0)
rest	predominant (2)/ not predominant (0)[6]	increases (1)/ decreases (-1)/ same (0)	increases (1)/ decreases (-1)/ same (0)
comfort	predominant (2)/ occurs yes (1)/ occurs no (0)	increases (1)/ decreases (-1)/ same (0)	increases (1)/ decreases (-1)/ same (0)
breed	predominant (2)/ occurs yes (1)/ occurs no (0)	increases (1)/ decreases (-1)/ same (0)	increases (1)/ decreases (-1)/ same (0)
vigilance	predominant (2)/ occurs yes (1)/ occurs no (0)	increases (1)/ decreases (-1)/ same (0)	increases (1)/ decreases (-1)/ same (0)
agonistics	predominant (2)/ occur yes (1)/ occur no (0)	increase (1)/ decrease (-1)/ same (0)	increase (1)/ decrease (-1)/ same (0)
shakes/ displays	occur yes (1)/ occur no (0)	increase (1)/ decrease (-1)/ same (0)	increase (1)/ decrease (-1)/ same (0)
posture changes	occur yes (1)/ occur no (0)	increase (1)/ decrease (-1)/ same (0)	increase (1)/ decrease (-1)/ same (0)
heart rate	increases (1)/ undulates 'regularly' (0)/ decreases (-1)	increases (1)/ decreases (-1)/ same (0)	increases (1)/ decreases (-1)/ same (0)
Pre-visit: The Conspecific Movement Measure (CMM; q.v.) determined extent of conspecific movement prior to human visitation (from absence of conspecific movement to constant movement of more than 15 conspecifics per 10 s)			

■ A 'Short' Guide to Reading Topography Charts

The **topography charts** described on the following pages (see fig. 5.3.1-2 for an example[7]) were compiled to gain a comprehensive impression of focal-animal comportment prior to, during, and after human visitation. Additionally, they permitted an assessment of responses to conspecific and – less prominently, due to much rarer occurrence – predator/ aircraft disturbance. These charts were appraised, and findings were summarised for each behaviour, posture, and heart rate as specified in the respective sections below.

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[6] For resting behaviour to be truly resting, it was assumed that predominance was required.

[7] For the complete 'package', see appendix 5.3.1-1.

Figure 5.3.1-2: Topography Chart – Behavioural, Postural, and Heart Rate Topography before, during, and after Human Visitation.

General order of chart: Each chart consists of **6 graphs grouped into 3 parts** (upper: 1a, b; middle: 2a, b; lower: 3a, b).

Graphs 1a, 2a, and 3a constitute ‘comportment graphs’ (FA behaviour, posture, and heart rate), while 1b, 2b, and 3b represent ‘disturbance graphs’ (human, conspecific, and predator/ aircraft).

Each graph represents a 10-minute time span; and graphs within the same part depict the same time span.

The **upper part** comprises information on focal-animal comportment (1a) before human visitation, i.e., FAs experience only ‘natural’ disturbance (1b).

The **middle part** shows focal-animal comportment (2a) during human visitation accompanied by ‘natural’ disturbance (2b).

The **lower part** provides information on focal-animal comportment (3a) after human visitation; again FAs are subjected to ‘natural’ disturbance only (3b).

Conspecific movement at 3 distances from the focal animal’s nest as well as conspecific presence at the focal animal’s nest were summed up for 10 s-intervals throughout the session.

Axes of the chart: In all graphs, time (in seconds) is denoted on the x-axis. For better alignment of focal-animal parameters with those of potential ‘disturbances’, time is displayed at the top of disturbance graphs (at maximum y-axis level).

In comportment graphs, the primary y-axis (left-hand) depicts changes in focal-animal behaviour and posture. Heart rate (in beats per 20 s) is tied to the secondary y-axis (right-hand).

In disturbance graphs, the primary y-axis depicts changes in numbers of conspecifics present (per 10 s), while the secondary y-axis is scaled according to the Visiting Stage Performance Indicator Value (VS-PIV, q.v.).

How to read the chart: The **titles** provide information on visiting regime. Furthermore, the focal animal’s identity code, the date of visitation and the time of day (mv = morning visit, av = afternoon visit) are given.

As outlined above (tab. 5.3.1-5), focal-animal behaviour and posture were coded numerically. Focal-animal behaviour (with the exception of shakes and displays) is represented by a bold black line (resulting from a dot placed for each second). Shakes and displays (disturbance indicators quoted in the literature) are symbolised by ‘spiked circles’.

Posture is depicted as a line of grey dots.

Focal-animal heart rate is shown as a prominent black dot every 20 s. Dots represent sum of heartbeats counted[1] in the 20 s-interval preceding that point.

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8 Heart rate is not depicted by bmp-values as these would have artificially inflated the ‘undulations’: 1 beat difference per 20 s-interval results in 3 beats difference per bmp-value.

What's There to See – Comportment Graphs:

The longer the focal animal remains within the same behaviour system/ keeps the same posture, the longer the lines remain unbroken.

Changes between behaviour systems/ postures cause the line to jump from one 'horizon' to the next.

Frequent disruptions of the 'behaviour line' by switches between two or more behaviour systems give the impression of 'scattered' behaviour (see box 5.3.1-1).

The succession of heart rate dots likewise undulates suavely if counts are similar, while abrupt changes in number of beats per 20 s are perceived as 'spikes'.

Human visitation (or its absence) is visualised as a continuous, dark line (graphs 1b, 2b, 3b). In the absence of humans (prior to and after visitation), this line runs along the x-axis. During visitation, the line rises/ falls between visiting stages, while plateaux represent the stages themselves (with approaches/ retreat also represented by a straight line). Please note that visiting stages are not drawn to scale (15 m, 5 m, and 3 m), and that visiting stages are depicted unweighted by visitor number and conduct, as the numbers on the respective axis code for the Visiting Stage Performance Indicator Value (q.v.).

Conspecific 'stationary' presence at the focal-animal nest and conspecific movement at three distances from the focal-animal nest are represented by blocks of different patterns and/ or shadings (see within-graph legend for details). Blocks have been stacked on top of one another to give an impression of 'overall conspecific presence' per 10 s. Within each block, conspecifics closest to the FA (1. standing or 2. moving in nest zone a) are above those further away (3. moving in nest zone b, 4. moving in nest zone c).

Ad-lib. observations of predator/ aircraft (symbols) disturbance are displayed below the timeline (x-axis at the top) of each disturbance graph, as applicable. Whenever possible, differentiations (e.g., skua low overflight, skua on ground) are provided (specification as text).

What's There to See[9] - Disturbance Graphs:

The closer the visitor gets to the focal animal, the closer the line draws to the focal-animal parameters depicted immediately above.

The greater the sum of conspecifics present per 10 s-interval, the higher the block. Within the block, conspecifics are arranged according to distance from the FA (numbers for nest zone a at the top, followed by those in nest zone b, numbers for nest zone c at the bottom).

Missing data on focal-animal behaviour and posture, as well as on conspecific presence, are represented by crosshatched columns. Columns covering the entire height of the graph indicate that no information whatsoever exists for the respective period of time. Lower columns have been used to depict partial loss of information (e.g., focal-animal behaviour unavailable, but information on posture retained). As a rule of thumb, longer stretches of data loss at the beginning/ end of sessions result from recordings not having started yet/ having ended already. Throughout a session, short stretches point to passing conspecifics temporarily hiding the (head of the) focal animal.

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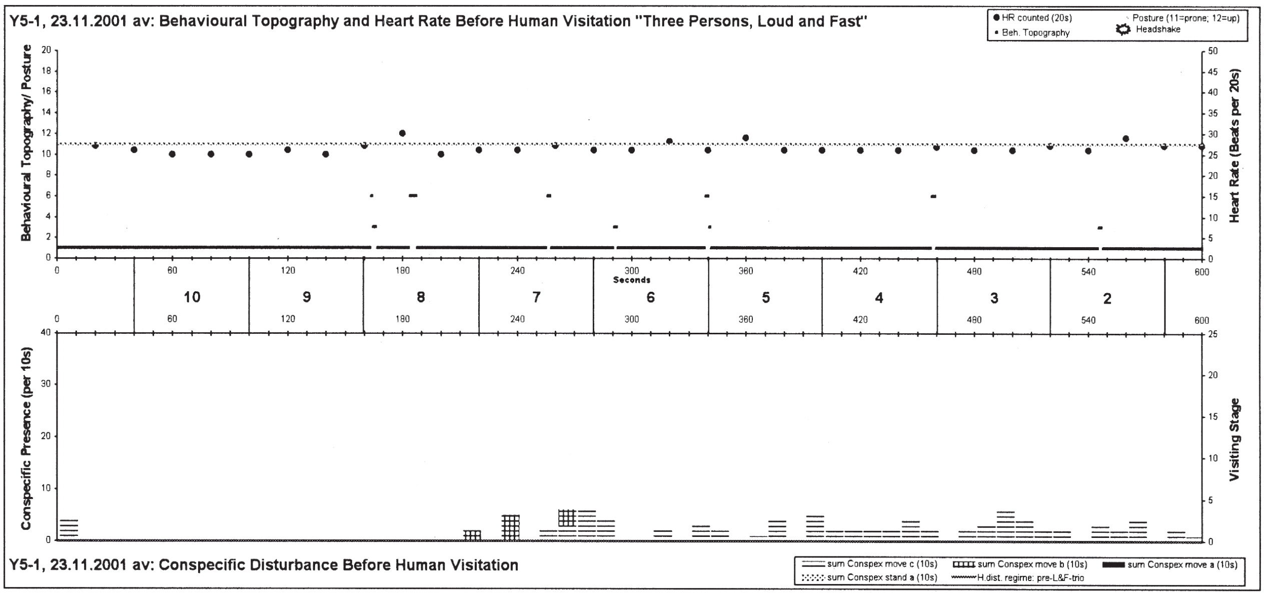
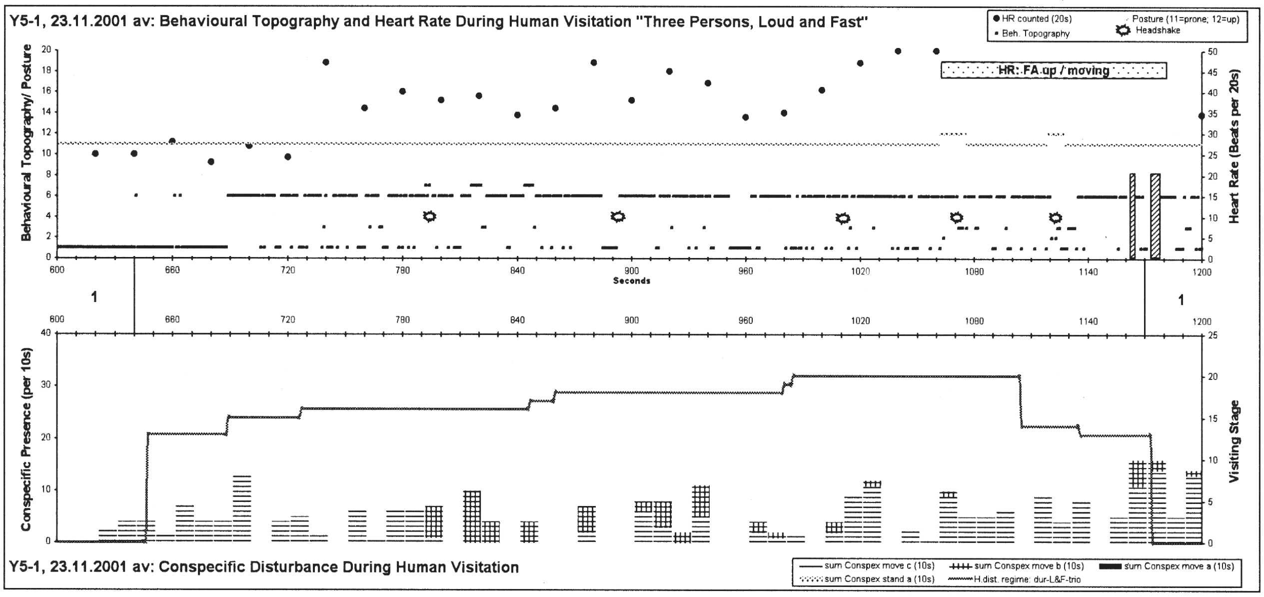
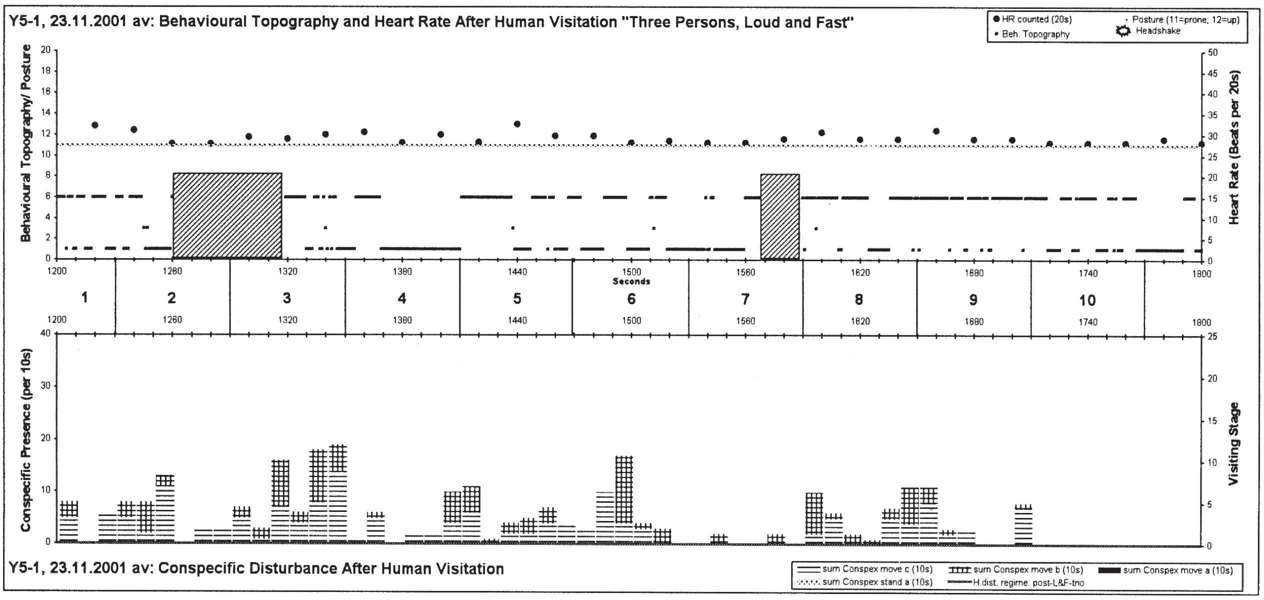
[9] Duration of predator presence/ aircraft noise has been written into the graphs.

Figure 5.3.1-2: Behavioural Topography, Heart Rate, and Conspecific Disturbance before, during and after Human Visitation. The figure shows an exemplary chart obtained from Y5-1 on 23 Nov. 2001 (see text for explanations).







Missing heart rate data are depicted as slim horizontal rectangles representing the extent of data loss. Within these rectangles, cause of data loss is specified (e.g., no records yet; indistinct, bird up/ moving).

Information on the whereabouts of the human visitor(s) was available at all times.

Abbreviations used in the charts:
pre: before visitation, **dur:** during visitation, **post:** after visitation;
mv: morning visit, **av:** afternoon visit;
solo: one visitor, **trio:** three visitors;
S&S: silent and slow, **L&F:** loud and fast;
HR: heart rate
conspex: conspecifics

5.3.1.1.2 Presentation of Results

Tabulated results: Due to several factors[10] , results for the different parameters (behaviour systems, postures, heart rate) are based on a differing number of recorded sessions. Furthermore, different numbers of sessions were recorded in each regime. For comparisons, observed values were therefore complemented by their respective proportions[11] , even though it is acknowledged that low observed numbers make for awkward proportions.

Only the **'proportional tables'** (including information on total number of sessions proportions are based on) are presented in this chapter; the respective 'observed tables' are found in appendix 5.3.1-2. Proportions based on less than 5 sessions were excluded or – in the case of data on heart rate and conspecifics – made explicit (1 of 4 instead of 25 %).

N.b.: Proportional entries do not necessarily add up to 100 %, as complementary classes (Yes/ No in pre-visit tables) as well as the class 'no change' (in during- and post-visit tables) have been omitted.

Mean-period values: Tables showing pre-, during- and post-visit values for each of the 2 min-intervals (before, after) and each of the visiting stages (during visitation), additionally provide average values per period (mean-period values) in the last column ('right end'). Mean values were calculated to assess whether they adequately reflected responses observed in each of the shorter intervals (for pre- and post-visitation: 2 min-intervals; for during-visitation: visiting stages).

Mean **pre-visit** values should reflect focal-animal 'general state' ('baseline') before presentation of the disturbance stimulus (human visitor). As far as mean **during-** and **post-visit** values are concerned, the procedure should enable comparison of post-visit to during-visit responses, i.e., they should serve to capture focal-animal 'general state' during and after subjection to the disturbance stimulus. As stimulus intensity varied during visitation (e.g., different distances; stay vs. approach) – and might have been perceived as 'waning', rather than 'gone abruptly' during the post-visit period – adequacy of these 'single key-values' will be critically discussed (chapter 6.1.1.2.3).

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[10] for behaviour: e.g., camera angle, obstructing conspecifics, obstructing neighbours; for heart rate: e.g., temporary equipment failure, illegibility of signal, bird losing contact with the artificial egg by getting up

[11] Proportions depict the number of sessions during which the required focal-animal comportment-category (yes/ no; predominant/ occurring/ absent) was observed divided by total number of sessions.

Colour codes: Throughout this section, two sets of colour codes are used to distinguish different proportional classes. Proportions obtained **prior to visitation** constituted the 'baseline' for later comparisons (tab. 5.3.1-6). To prevent accidental confusion with results on changes observed during or after human visitation, colours coding for different proportional classes observed before the visit were taken from the **blue/ green spectrum**.

Table 5.3.1-6: Proportional Classes: Colour Codes for Proportions Calculated for Each Behaviour System, Posture, and Heart Rate <u>prior to</u> Human Visitation. Proportions depict the number of sessions during which the required focal-animal comportment-category (yes/ no; predominant/ occurring/ absent) was observed divided by total number of sessions.

Proportional Class	Name of Colour	Hue of Colour
75 % to 89 % (and above)	Aquamarine	🟦
60 % to 74 %	Bright Green	🟩
45 % to 59 %	Turquoise	🟦
30 % to 44 %	Light Green	🟩
15 % to 29 %	Light Turquoise	🟦
0 % to 14 %	White	

The colour code for **change classes** (increases/ decreases as compared to pre-visit behaviour), in contrast, follows the 'rainbow-gradient': **red-orange-yellow-white** (tab. 5.3.1-7).

Table 5.3.1-7: Proportional Change Classes: Colour Codes for Proportions of Increases/ Decreases in Each Behaviour System, Posture, and Heart Rate <u>during</u> and <u>after</u> Human Visitation. Proportions depict the number of sessions during which the required focal-animal response was observed divided by total number of sessions.

Proportional Change Class	Name of Colour	Hue of Colour
75 % to 89 % (and above)	Red	🟥
60 % to 74 %	Light Orange	🟧
45 % to 59 %	Golden	🟧
30 % to 44 %	Yellow	🟨
15 % to 29 %	Light Yellow	🟨
0 % to 14 %	White	

Order of Presentation: This section starts with an appraisal of extent and persistence of conspecific movement prior to human visitation to establish the level of 'natural disturbance' present at the beginning of human visitation.

Following this, the same **order of presentation** has been adopted for each behaviour system, posture, and heart rate: Results on **pre-, during-, and post-visitation** are followed by those on **conspecific, skua and aircraft disturbance**. Within each of these 'packages', the <u>main effect</u> is presented first for ***all regimes*** together, followed by results on ***specific regimes***. Subsequently, <u>lesser effects</u> – if applicable – are mentioned in the same order (all regimes together, specific regimes).

As regards the **pre-visit period**, <u>predominance</u> across several 2 min-intervals is presented for resting as well as vigilance behaviour. **During**- and **post-visitation**, the comportment parameters resting, vigilance, and heart rate were additionally subjected to an examination of <u>antidirectional</u> (comportment parameters simultaneously changing in the opposite direction) as well as <u>syndirectional changes</u> (comportment parameters simultaneously changing in the same direction).

The section concludes with a number of questions arising from visual appraisal, which are addressed in the subsequent sections of this chapter.

5.3.1.2 Potential Impact of Conspecific Movement before Human Visitation on Focal-Animal Comportment during and after Visitation

Using the **conspecific movement measure** (CMM, tab. 5.3.1-4), conspecific movement prior to human visitation was examined for each session.

Summing up, high conspecific movement prior to human visitation needs to be kept in mind with respect to responses exhibited by FAs-$C_{1,2}$, but is thought unlikely to explain differences found at the other three regimes.

General findings: Values for class 1 ('constant movement of less than 5 conspecifics per 10 s interval') and class 3 ('constant movement of 5-15 conspecifics per 10 s interval') were lower than those for the respective intermittent movements (classes 0 and 2, resp.), while the reverse was true with respect to classes 5 and 4 ('constant/ intermittent movement of more than 15 conspecifics per 10 s interval').

Conspecific movement **before visits** was generally fluctuating across 2 min-intervals (tab. 5.3.1-9). Table 5.3.1-8 shows that for ***all regimes***, the majority of conspecific movement prior to human visitation conformed to class 2 of the conspecific movement measure, and was thus characterised by 'intermittent movement of 5 to 15 conspecifics per 10 s count'. The second highest value (class 0) comprised none to very low ('intermittent movement of less than 5 conspecifics') conspecific movement.

As for ***specific regimes***, the most striking exception was found for FAs-$C_{1,2}$, with the second highest value conforming to the highest class (5), which captured 'constant movement of more than 15 conspecifics per 10s count' (tab. 5.3.1-8). An influence of spatial differences (different locations of regimes within the colony) did not seem likely, as FAs-Y inhabited roughly the same area in the following year, but showed a distinct pattern from that found for FAs-$C_{1,2}$.

With respect to FAs-X and FAs-Y, the two highest values were rather similar, while the values for 'none to very low movement' in FAs-B_1 and FAs-$C_{1,2}$ were less than half of the respective maximum values (class 2). Concerning FAs-B_1, values for the highest two classes (4 and 5) were equally low at only 6 %, while only for FAs-Y, these classes remained unoccupied prior to human visitation.

Table 5.3.1-8: Pre-Visit Intensity of Conspecific Movement as Characterised by the Conspecific Movement Index (CMM). For each row, the two highest values are marked in bold print. CMM: Conspecific Movement Measure; 0-1: none to low, 2-3: intermediate, 4-5: high (for details see text); n (int.): total number of pre-visit intervals the proportion is based on. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

CMM pre-visit	0	1	2	3	4	5
FAs-allReg n (int.) = 218	**23.39**	9.17	**35.32**	14.22	5.96	11.93
FAs-B_1 n (int.) = 63	**20.63**	14.29	**44.44**	7.94	6.35	6.35
FAs-$C_{1,2}$ n (int.) = 69	14.49	4.35	**34.78**	14.49	10.14	**21.74**
FAs-X n (int.) = 60	**33.33**	5.00	**26.67**	20.00	3.33	11.67
FAs-Y n (int.) = 26	**30.77**	19.23	**34.62**	15.38	0.00	0.00

Table 5.3.1-9 gives the respective proportions per 2 minute pre-visit interval. Note that the classes have been pooled to provide a 'condensed' overview of 'none to low' (0-1), 'medium' (2-3), and 'high' (4-5) numbers of moving conspecifics, respectively.

Table 5.3.1-9: Conspecific Movement <u>before</u> Human Visitation. For comparison, proportional values are shown. CMM: Conspecific Movement Measure; **0-1**: nonexistent to low, **2-3**: moderate to intermediate, **4-5**: high to very high; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: based on less than 5 sessions and thus excluded.

Conspecific Movement (%) – 'condensed'	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg CMM **0-1**	48.39	21.95	39.13	28.57	29.41	32.57
FAs-allReg CMM **2-3**	35.48	68.29	43.48	53.06	45.10	49.54
FAs-allReg CMM **4-5**	16.13	9.76	17.39	18.37	25.49	17.89
FAs-B$_1$ CMM **0-1**	*no %*	33.33	53.85	11.76	29.41	34.92
FAs-B$_1$ CMM **2-3**	*no %*	66.67	38.46	58.82	58.82	52.38
FAs-B$_1$ CMM **4-5**	*no %*	0.00	7.69	29.41	11.76	12.70
FAs-C$_{1,2}$ CMM **0-1**	18.18	0.00	20.00	42.86	12.50	18.84
FAs-C$_{1,2}$ CMM **2-3**	36.36	92.31	40.00	42.86	37.50	49.28
FAs-C$_{1,2}$ CMM **4-5**	45.45	7.69	40.00	14.29	50.00	31.88
FAs-X CMM **0-1**	41.67	25.00	50.00	25.00	50.00	38.33
FAs-X CMM **2-3**	58.33	50.00	41.67	58.33	25.00	46.67
FAs-X CMM **4-5**	0.00	25.00	8.33	16.67	25.00	15.00
FAs-Y CMM **0-1**	*no %*	*no %*	33.33	50.00	33.33	50.00
FAs-Y CMM **2-3**	*no %*	*no %*	66.67	50.00	66.67	50.00
FAs-Y CMM **4-5**	*no %*	*no %*	0.00	0.00	0.00	0.00
$n_{(sess.)}$ FAs-allReg	31	41	46	49	51	n.a.
$n_{(sess.)}$ FAs-B$_1$	4	12	13	17	17	n.a.
$n_{(sess.)}$ FAs-C$_{1,2}$	11	13	15	14	16	n.a.
$n_{(sess.)}$ FAs-X	12	12	12	12	12	n.a.
$n_{(sess.)}$ FAs-Y	4	4	6	6	6	n.a.

Looking at ***all regimes*** together, proportions for <u>none to low</u> numbers of moving conspecifics **before human visitation** ranged from 22 % to 48 % (mean pre-visit: 33 %) in five 2 min-intervals. Proportions for <u>medium</u> numbers of moving conspecifics ranged from 35 % to 68 % (mean pre-visit: 50 %), while proportions for <u>high</u> numbers ranged from 10% to 25 % (mean pre-visit: 18 %).

<u>Immediately prior to human visitation</u> (2-1 minutes), conspecific movement at ***all regimes*** was nonexistent to low (<u>low</u> numbers) for 29 % of all sessions. It was moderate to intermediate (<u>medium</u> numbers) for 45 %, and high to very high (<u>high</u> numbers) for 25 %.

As for ***specific regimes***, mean proportions for <u>medium</u> numbers of moving conspecifics were similar, but regimes differed with respect to the other values: In the vicinity of FAs-C$_{1,2}$ mean proportions for <u>low</u> numbers of moving conspecifics were less prominent, and more prominent near FAs-Y, while those for <u>high</u> numbers of moving conspecifics were distinctly higher at FAs-C$_{1,2}$, slightly lower at FAs-B$_1$, and nonexistent at FAs-Y.

5.3.1.3 'Scattered' Behaviour

<u>**Summing up**</u>, scattered behaviour was frequently observed <u>prior to visitation</u> (FAs-allReg mean pre-visit: 32 %). <u>Increases</u> (as compared to pre-visit) constituted the <u>main change</u> observed in scattering both during (max. during-visit value FAs-allReg: +46 %) and after visitation (max. post-

visit value: +38 %). It was predominantly the behaviour systems of breeding and agonistics that contributed to the scattering. Decreased scattering during-visitation mainly occurred when the focal bird's behaviour had been divided between several systems prior to human visitation; generally, a decrease in scattering was caused by vigilance becoming the predominant behaviour system exhibited.

Comparing disturbance types (human visitation, conspecific disturbance, skua/ aircraft disturbance; FAs-allReg), scattering increased in nearly half of all sessions during **human** visitation and more than a third post-visit, with mean during-visit values (+27 %) slightly lower than mean post-visit ones (+31 %).

Towards **conspecifics**, increased scattering did not constitute a consistent reaction: It was never observed for conspecific 'stationary' presence at the focal nest, once (FA-B_1, of 12 sessions) in 45 sessions for conspecific movement at the focal nest, and 6 times in 49 sessions (FAs-B_1: 5 of 15; FAs-X: 1 of 12) for conspecific movement irrespective of distance from the focal nest. It never occurred in response to **skua/ aircraft** disturbance.

Comparing visiting stages and post-visit 2 min-intervals (FAs-allReg), the **highest mean-values** for increased scattering (+46 % and +43 %, resp.) were found at 5 m and at 3 m distance from the focal animal's nest during visitation, followed by values obtained in the second (3-4 min; +38 %) and first (1-2 min; +37 %) post-visit intervals.

Comparing FAs subjected to different regimes, values for increased scattering during visitation calculated for FAs-Y (3 P, L&F) frequently reached higher change classes than those of the other regimes; the **highest value** was obtained for visiting stage 'visitor at 3 m' (+80 %).

Both during- and post-visit, FAs from different regimes showed temporal differences with respect to **peak values**. During-visit, these were reached first by FAs-B_1 (1 P, L&F; 47 %, visitor at 5 m), followed by FAs-$C_{1,2}$ (mainly 1 P, S&S; 57 %, visitor at 3 m) and FAs-Y (3 P, L&F; 80 %, visitor at 3 m), and last by FAs-X (3 P, S&S; 42 %, visitor retreat). Post-visit, values peaked first in FAs-X (+50 %, 1-2 min post-visit), followed by FAs-$C_{1,2}$ (+43 %, 3-4 min post-visit), and FAs-B_1 (+50 %, 5-6 min post-visit). With respect to FAs-Y, there was no peak[12] value.

"Curiouser and Curiouser": While decreased scattering was not observed in all regimes, and values were generally lower than for increases, FAs-B_1 were exceptional, in that values for decreased scattering frequently exceeded those for increases. Across all visiting stages/ post-visit intervals, values for increased scattering were higher than for decreases at the visiting stages 'visitor at 5 m' and 'visitor at 3 m', and during the first eight minutes post-visit (intervals 1 to 4).

General findings: In only 2 of the 51 sessions recorded, behaviour was never scattered throughout the session (i.e., before, during, or after human visitation). Both of these had been recorded at the same nest (B3), but from different focal animals (B3-1, 26.11.2000av; B3-2, 20.11.2000mv; see appendix 5.3.1-1).

Before human visitation, behaviour was classified as either scattered or not scattered for each 2 min-interval recorded (10-9 min pre-visit, 8-7 min pre-visit, etc.).

Looking at ***all regimes*** (appendix 5.3.1-1), in 10 of 51 sessions, scattering persisted throughout the pre-visit period. It was predominantly the behaviour systems of breeding and agonistics that contributed to the scattering. Intermittent scattered behaviour ('yes' in one interval, 'no' in the

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[12] 33 % of 6 and 40 % of 5 both amounting to 2 sessions

following one) was observed in approximately one third of all sessions (mean pre-visit: 32 %, range: 29 % to 35 %; tab. 5.3.1-10).

Immediately before the visit (2-1 min pre-visit), scattered behaviour occurred in 33 % of all sessions.

Concerning ***regime differences***, values obtained from FAs-$C_{1,2}$ were above those seen at the other regimes (with the exception of the fourth pre-visit interval). This resulted in the highest mean pre-visit value for scattering (45 %) for FAs-$C_{1,2}$. The lowest values for scattering prior to human visitation were found in FAs-Y (mean pre-visit: 13 %); and continuously scattered behaviour was not observed in these focal birds (appendix 5.3.1-1).

Table 5.3.1-10: Occurrence and Prevalence of Scattered Behaviour before Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; occurs: occurring; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Scattering (%)	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg **Occurs**	31.25	34.88	28.89	31.25	33.33	31.92
FAs-B_1 **Occurs**	*no %*	23.08	23.08	35.29	31.25	28.17
FAs-$C_{1,2}$ **Occurs**	40.00	61.54	50.00	30.77	42.86	45.03
FAs-X **Occurs**	41.67	27.27	16.67	41.67	33.33	32.12
FAs-Y **Occurs**	16.67	16.67	16.67	0.00	16.67	13.33
$n_{(sess.)}$ FAs-allReg	32	43	45	48	48	n.a.
$n_{(sess.)}$ FAs-B_1	4	13	13	17	16	n.a.
$n_{(sess.)}$ FAs-$C_{1,2}$	10	13	14	13	14	n.a.
$n_{(sess.)}$ FAs-X	12	11	12	12	12	n.a.
$n_{(sess.)}$ FAs-Y	6	6	6	6	6	n.a.

During human visitation (tab. 5.3.1-11) scattering of behaviour increased in most sessions as compared to pre-visit behaviour.

Looking at all sessions from ***all regimes***, increased scattering ranged from +9 % to +46 % (mean during-visit: +27 %). Increases in scattering became more prominent as soon as the visitor(s) had arrived at 15 m (+23 %), and persisted until the visiting stage of retreat (+36 %). The highest values for increased scattering (+46 % and +44 %, resp.) were found at 5 m and at 3 m distance from the focal animal's nest, followed by that during visitor retreat (+36 %).

Table 5.3.1-11 shows only slight ***regime differences*** with respect to the order described above. For FAs-Y, the mean during-visit value for increased scattering was considerably higher than at the other regimes (+42 %), since values for FAs-Y reached higher change classes than those calculated for other regimes at the majority of visiting stages (exception: approach to 15 m; along colony – post).

Mean during-visit values were nearly equal for FAs-$C_{1,2}$ and FAs-X (+27 % and +26 %, resp.), and lowest for FAs-B_1 (+23%). Values for increased scattering during changes of distance (thrice approach, retreat) rose continuously with respect to FAs-B_1 and FAs-$C_{1,2}$ (approach to 15 m < approach to 5 m < approach to 3 m < retreat), while for FAs-X, they were elevated earlier, remained the same for both approaches and rose again during retreat (approach to 15 m < approach to 5 m = approach to 3 m < retreat). Concerning FAs-Y, values were zero fpr approach to 15m and equally high at the following three changes of distance (+50 %). For FAs-C$_{1,2}$ and FAs-Y[13], persistence of increased scattering continued into the visiting stage of ‘visitor along colony – post-visit’. While there was little difference between the last two stages at FAs-C$_{1,2}$ (+29 % vs. +27 %), a distinct lessening of response was observed at FAs-Y (+50 % vs. +17 %).

A decrease in scattering (as compared to pre-visit behaviour) was not observed at ***all regimes***; consequently, no overall trend is described (FAs-allReg: n.a.). As for ***regime differences***, decreased scattering was observed in FAs-B$_1$ (mean during-visit: -27 %) and – albeit on a much smaller scale – in FAs-X (mean during-visit: -7 %), but not in FAs-C$_{1,2}$ and FAs-Y.

Please note that FAs-B$_1$ were exceptional in that mean decreases in scattering actually surpassed mean increases.

Decreased scattering mainly occurred when the focal bird’s behaviour had been divided between several systems prior to human visitation; generally, a decrease in scattering was caused by vigilance becoming the predominant behaviour system exhibited (appendix 5.3.1-1).

Table 5.3.1-11: Occurrence and Prevalence of Scattered Behaviour during Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, **–**: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded. **N.b.:** Except for two sessions from FAs-B$_1$ (% not shown), the visiting stages ‘visitor along colony (20-25 m)’ immediately pre-visit and post-visit applied only to FAs-C$_{1,2}$ and FAs-Y.

Scattering (%)	**visitor along colony (20-25m)**	**visitor approach to 15m**	**visitor @ 15m**	**visitor approach to 5m**	**visitor @ 5m**	**visitor approach to 3m**	**visitor @ 3m**	**visitor retreat**	**visitor along colony (20-25m)**	**mean during-visit**
FAs-allReg **+**	13.04	8.51	23.40	23.91	45.65	27.08	43.48	36.17	23.81	27.23
FAs-B$_1$ **+**	*no %*	6.67	21.43	14.29	46.67	20.00	40.00	33.33	n.a.	22.80
FAs-C$_{1,2}$ **+**	6.67	7.14	20.00	21.43	46.15	26.67	57.14	28.57	26.67	26.72
FAs-X **+**	n.a.	16.67	25.00	25.00	33.33	25.00	16.67	41.67	n.a.	26.19
FAs-Y **+**	33.33	0.00	33.33	50.00	66.67	50.00	80.00	50.00	16.67	42.22
FAs-allReg **–**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B$_1$ **–**	*no %*	-20.00	-35.71	-21.43	-26.67	-20.00	-33.33	-33.33	n.a.	-27.21
FAs-C$_{1,2}$ **–**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
FAs-X **–**	n.a.	-8.33	-8.33	-8.33	-8.33	0.00	-16.67	0.00	n.a.	-7.14
FAs-Y **–**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$n_{(sess.)}$ FAs-allReg	23	47	47	46	46	48	46	47	21	n.a.
$n_{(sess.)}$ FAs-B$_1$	2	15	14	14	15	15	15	15	0	n.a.
$n_{(sess.)}$ FAs-C$_{1,2}$	15	14	15	14	13	15	14	14	15	n.a.
$n_{(sess.)}$ FAs-X	0	12	12	12	12	12	12	12	0	n.a.
$n_{(sess.)}$ FAs-Y	6	6	6	6	6	6	5	6	6	n.a.

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[13] Visitor route depended on location of group relative to starting point of visitor(s), and the stages ‘visitor along colony – pre/ post’ did not apply to groups B and X (see Chapter 3.2.2.3, fig. 3-25).

After the visit (tab. 5.3.1-12), increases in scattering were observed far more frequently than decreases; they occurred at all regimes and persisted until the end of the 10 min post-visit period. The mean post-visit value for increased scattering (+31 %) was slightly higher than the mean during-visit value (+27 %).

For ***all regimes*** together, the proportion of sessions during which increased scattering (as compared to pre-visit) was observed remained approximately equal to that during visitor retreat (tab. 5.3.1-11) for the first and second 2 min-intervals (37 % and 38 % for minutes 1-2 and 3-4, resp.) In the following minutes (5-6, 7-8, and 9-10), the value declined progressively (+32 %, +29 %, and +20 %, resp.).

Table 5.3.1-12 shows temporal differences among ***specific regimes*** with respect to peak values for increased scattering, but within each regime the lowest value was found in the last post-visit interval[14].

While FAs-C$_{1,2}$ and FAs-X showed little difference between mean values for increased scattering during- (tab. 5.3.1-11) and post-visit (tab. 5.3.1-12), the mean post-visit value obtained from FAs-Y was lower, whereas that calculated for FAs-B$_1$ was higher than the respective during-visit means.

After human visitation, decreased scattering (as compared to pre-visit behaviour) was not observed at ***all regimes***; therefore no overall trend is described. As for ***specific regimes***, a decrease was observed in one bird of FAs-X (appendix 5.3.1-1) (mean: -9 %) as well as in some sessions from FAs-B$_1$ (mean: -17 %). As for the latter, mean post-visit decreases in scattering amounted to less than half of mean post-visit increases (+38 %) of FAs-B$_1$, contrary to values obtained during human visitation (resulting in mean during-visit values of -27 % and +23 %, resp.). Decreased scattering was never observed in FAs-C$_{1,2}$ and FAs-Y.

Table 5.3.1-12: Occurrence and Prevalence of Scattered Behaviour after Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, **—**: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Scattering (%)	**1-2min post-visit**	**3-4min post-visit**	**5-6min post-visit**	**7-8min post-visit**	**9-10min post-visit**	**mean post-visit**
FAs-allReg **+**	36.73	38.30	31.82	28.57	20.00	31.08
FAs-B$_1$ **+**	40.00	46.67	50.00	28.57	23.08	37.66
FAs-C$_{1,2}$ **+**	25.00	42.86	28.57	23.08	23.08	28.52
FAs-X **+**	50.00	25.00	16.67	30.00	10.00	26.33
FAs-Y **+**	33.33	33.33	*no %*	40.00	*no %*	35.56
FAs-allReg **–**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B$_1$ **–**	-6.67	-13.33	-21.43	-21.43	-23.08	-17.19
FAs-C$_{1,2}$ **–**	0.00	0.00	0.00	0.00	0.00	0.00
FAs-X **–**	-8.33	-8.33	-8.33	-10.00	-10.00	-9.00
FAs-Y **–**	0.00	0.00	*no %*	0.00	*no %*	0.00
n$_{(sess.)}$ FAs-allReg	49	47	44	42	40	n.a.
n$_{(sess.)}$ FAs-B$_1$	15	15	14	14	13	n.a.
n$_{(sess.)}$ FAs-C$_{1,2}$	16	14	14	13	13	n.a.
n$_{(sess.)}$ FAs-X	12	12	12	10	10	n.a.
n$_{(sess.)}$ FAs-Y	6	6	4	5	4	n.a.

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[14] With respect to group Y, increased scattering was observed in 1 session out of 4 during both the third and the fifth post-visit interval.

Post-visit decreases in scattering were mainly associated with increased resting behaviour (appendix 5.3.1-1).

Scattering was not a response exhibited towards **conspecific** presence at the focal nest. In response to conspecific movement at the focal nest, increased scattering was found in one session from FAs-B_1; increased conspecific movement (irrespective of distance from the focal nest) caused increased scattering during 5 sessions from FAs-B_1 and 1 session from FAs-X. The few occurrences of **skua** disturbance (low overflight or on ground) and **aircraft** noise within these datasets did not elicit increased scattering in any of the sessions.

Decreased scattering was not observed for any of these disturbance types (appendix 5.3.1-1).

5.3.1.4 Resting Behaviour

Summing up, predominance of resting behaviour was frequently observed prior to visitation (FAs-allReg mean pre-visit: 40 %). Decreases (as compared to pre-visit) constituted the main change observed in resting behaviour both during (max. during-visit value FAs-allReg: -85 %) and after visitation (max. post-visit value: -47 %).

Comparing disturbance types (human visitation, conspecific disturbance, skua/ aircraft disturbance; FAs-allReg), resting behaviour decreased in all sessions but three during **human** visitation (mean during-visit value -63 %). Mean post-visit values for decreased resting behaviour were considerably lower (-40 %).

Decreased resting behaviour did not constitute a consistent reaction towards **conspecifics**, but was found to occur at selected sessions (particularly in FAs-B_1; appendix 5.3.1-1). As a response to **skua** low overflights, it was observed in less than half the sessions, while skua presence on ground close to the focal nest elicited reduced resting behaviour in four cases out of five. **Aircraft** noise reduced resting behaviour in one of two focal birds concerned. For none of these disturbance types, increases in resting behaviour were ever observed.

Comparing visiting stages and post-visit 2 min-intervals (FAs-allReg), the **highest mean-values** for decreased resting behaviour (-85 % and -83 %, resp.) were invariably found during visitation; with maximum values at 3 m and at 5 m distance from the focal animal's nest, followed by values obtained during retreat (-80 %) and approach to 3 m (-78 %). Mean post-visit values, in contrast, were much lower (max. -47 %, 1-2 min post-visit).

Antidirectional changes during visitation predominantly concerned **vigilance**, in that decreased resting was accompanied by increased vigilance throughout the visit. **Breeding** behaviour 'replacing' resting behaviour was observed during visitor stay at 5 m and 3 m as well as during retreat. Increased **agonistic** behaviour coinciding with reduced resting behaviour was more common during the 'visit proper', commencing with the visitor's staying at 15 m, and subsiding with visitor retreat. After visitation, resting behaviour continued to be most prominently 'replaced' by **vigilance** behaviour, although the number of cases observed waned continuously (from 20 sessions during the first post-visit interval to 10 sessions during the fifth). The opposite conjunction (increased resting and decreased vigilance) attained prominence from the second post-visit interval onwards (3-10 min).

Decreased resting in conjunction with increased **breeding** as well as increased **comfort** behaviour was most prominent during the third post-visit interval (5-6 min), while 'replacement' by increased **agonistics** was notable in the first post-visit interval (1-2 min) only.

Syndirectional changes were only sporadically observed during- and post-visitation.

Comparing FAs subjected to different regimes, values for decreased resting behaviour calculated for FAs-B$_1$ and FAs-X during visitation frequently reached higher change classes than those of the other two regimes; the **highest value** was obtained from FAs-X for visiting stage 'visitor at 3 m' (100 %).

Both during- and post-visit, FAs from different regimes showed temporal differences with respect to **peak values**. During visit, these were reached first by FAs-B$_1$ (visitor at 5 m, -94 %), followed by FAs-C$_{1,2}$ (visitor approach to 3 m, -73 %), and 'trailed' jointly by FAs-X (-100 %) and FAs-Y (-80 %) at the visiting stage 'visitor at 3 m'.

After visitation, peak values for FAs-B$_1$ (-53 %), FAs-C$_{1,2}$ (-50 %), and FAs-Y (-50 %) were calculated for the first post-visit interval (1-2 min), with values for FAs-Y persisting into the second interval (3-4 min post-visit). In contrast, peak values for FAs-X (-50 %) fell into the second and third post-visit intervals (3-6 min).

"Curiouser and Curiouser": During visitation, increases (as compared to pre-visit) in resting behaviour were rare[15] (max. +5 % in FAs-C$_{1,2}$), and were not observed in FAs-Y. Post-visitation, however, they became more frequent (mean post-visit value: +18 %). While extent of increases never surpassed that of decreases for FAs-B$_1$, FAs-X, and FAs-Y, increases found for FAs-C$_{1,2}$ equalled decreases during the third (5-6 min: +21 % and -21 %) and fifth (9-10 min: +23 % and -23 %) post-visit intervals (tab. 5.3.1-17).

General findings: Resting behaviour in the sense of 'immobility on the nest' was observed in all sessions recorded. Prolonged resting, however, did not occur in all sessions. For establishment of the pre-visit baseline, the extent to which resting behaviour had been predominant was examined (tab. 5.3.1-14).

Before human visitation, resting behaviour was classified as either predominant or not predominant for each 2 min-interval recorded. For ***all regimes*** together, values for predominant resting ranged from 34 % to 46 % (mean pre-visit: 40 %; tab. 5.3.1-13).

Immediately before the visit (2-1 min pre-visit), resting behaviour was predominant in 34 % of all sessions.

Table 5.3.1-13: Extent of Predominance of Resting Behaviour before Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; Predom: predominant; n (sess.): number of sessions proportion is based on; n.a.: not applicable; no %: value based on less than 5 sessions and thus excluded.

Resting Behaviour (%)	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg **Predom**	40.63	39.53	45.65	40.82	34.04	40.13
FAs-B$_1$ **Predom**	*no %*	69.23	69.23	41.18	37.50	54.28
FAs-C$_{1,2}$ **Predom**	10.00	7.69	13.33	28.57	15.38	15.00
FAs-X **Predom**	50.00	45.45	58.33	41.67	50.00	49.09
FAs-Y **Predom**	50.00	33.33	50.00	66.67	33.33	46.67
$n_{(sess.)}$ FAs-allReg	32	43	46	49	47	n.a.
$n_{(sess.)}$ FAs-B$_1$	4	13	13	17	16	n.a.
$n_{(sess.)}$ FAs-C$_{1,2}$	10	13	15	14	13	n.a.
$n_{(sess.)}$ FAs-X	12	11	12	12	12	n.a.
$n_{(sess.)}$ FAs-Y	6	6	6	6	6	n.a.

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[15] that not being the 'curious' part

Concerning ***specific regimes***, for FAs-$C_{1,2}$ pre-visit predominance of resting behaviour was constantly lower (mean pre-visit: 15 %) than at the other regimes (means pre-visit: 54 %, 49 %, and 47 %, for FAs-B_1, FAs-X, and FAs-Y, resp.).

More extensive stretches of predominant resting behaviour (tab. 5.3.1-14) of 4 to 10 min (as well as within single 2 min-intervals) were not equally distributed across the regimes, and were least frequent in FAs-$C_{1,2}$. Additionally, sessions during which resting behaviour was never predominant in any of the 2 min-intervals before human visitation were most often observed in FAs-$C_{1,2}$. Most frequently, non-predominant resting behaviour was due to relatively high levels of vigilance or a combination of vigilance, breeding and agonistic behaviours (qq.v.).

Table 5.3.1-14: Consecutive Two-Minute Intervals during Which Resting Behaviour was Predominant before Human Visitation. Values on 5 to 1 intervals are presented cumulatively. Proportions in brackets represent the extent to which resting behaviour was never/ always predominant (100 % = n). 'never predominant': in none of the 2 min-intervals of a given session; always predominant: in all of the 2 min-intervals of a given session (includes sessions with less than five 2 min-intervals due to data loss); predominant: entirely uninterrupted or with very few and short interruptions; n: number of sessions recorded; 5 consecutive intervals = entire pre-visit period; o: empty category; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

Resting Behaviour predominant	for **5** consecutive intervals	for at least **4** consecutive intervals	for at least **3** consecutive intervals	for at least **2** consecutive intervals	for at least **1** interval/ **disjunct single** intervals	R **never** predominant	R **always** predominant
FAs-allReg (n=51 sessions)	5	9	17	21	32	19 (37 %)	9 (18 %)
FAs-B_1 (n=17 sessions)	1	4	7	10	12	5 (29 %)	4 (24 %)
FAs-$C_{1,2}$ (n=16 sessions)	o	o	2	2	6	10 (63 %)	1 (6 %)
FAs-X (n=12 sessions)	2	3	6	6	9	3 (25 %)	2 (17 %)
FAs-Y (n=6 sessions)	2	2	2	3	5	1 (17 %)	2 (33 %)

During human visitation, resting behaviour decreased in all sessions but three[16] (appendix 5.3.1-1). Decreased resting behaviour ranged from -24 % to -85 % (mean during-visit: -63 %; tab. 5.3.1-15).

Looking at ***all regimes***, decreases in resting behaviour as compared to pre-visit behaviour became more prominent as the visitor(s) approached to 15 m (with the proportion of sessions during which the bird responded rising from -24 % to -55 %) and persisted throughout the visit.

The decrease was most pronounced (i.e., observed in the greatest proportion of sessions recorded) while the visitor(s) remained at 3 m and 5 m distance from the focal animal (-85 % and -83 %, resp.), and only slightly less for visitor retreat as well as visitor approach to 3 m (-80 % and -78 %, resp.).

As for ***regime differences***, table 5.3.1-15 shows a slight delay in peak responses for FAs-$C_{1,2}$. Mean during-visit values were distinctly higher for FAs-B_1 and FAs-X (-81 %, -76 %) than for FAs-$C_{1,2}$ and FAs-Y (-54 %, -59 %), respectively.

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[16] During two of these, the focal animals had exhibited predominantly vigilance behaviour prior to visitation (from eight minutes and six minutes onwards, respectively). In the remaining session, the FA had engaged in preening prior to visitation so that vigilance had 'replaced' comfort, rather than resting behaviour.

Table 5.3.1-15: Occurrence and Prevalence of Resting Behaviour <u>during</u> Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, **–**: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded. **N.b.:** Except for two sessions from FAs-B$_1$ (% not shown), the visiting stages 'visitor along colony (20-25 m)' immediately pre-visit and post-visit applied only to FAs-C$_{1,2}$ and FAs-Y.

Resting Behaviour (%)	**visitor along colony (20-25m)**	**visitor approach to 15m**	**visitor @ 15m**	**visitor approach to 5m**	**visitor @ 5m**	**visitor approach to 3m**	**visitor @ 3m**	**visitor retreat**	**visitor along colony (20-25m)**	**mean during-visit**
FAs-allReg **+**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B$_1$ **+**	*no %*	0.00	6.25	6.25	0.00	5.88	0.00	5.88	n.a.	3.47
FAs-C$_{1,2}$ **+**	0.00	0.00	6.67	14.29	0.00	0.00	0.00	7.14	13.33	4.60
FAs-X **+**	n.a.	8.33	8.33	0.00	0.00	0.00	0.00	0.00	n.a.	2.38
FAs-Y **+**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
FAs-allReg **–**	-23.81	-55.10	-57.14	-64.58	-83.33	-78.00	-85.42	-79.59	-42.86	-63.32
FAs-B$_1$ **–**	*no %*	-64.71	-68.75	-75.00	-94.12	-82.35	-94.12	-88.24	n.a.	-81.04
FAs-C$_{1,2}$ **–**	-26.67	-50.00	-46.67	-42.86	-69.23	-73.33	-64.29	-71.43	-40.00	-53.83
FAs-X **–**	n.a.	-41.67	-50.00	-83.33	-91.67	-83.33	-100	-83.33	n.a.	-76.19
FAs-Y **–**	-16.67	-66.67	-66.67	-50.00	-66.67	-66.67	-80.00	-66.67	-50.00	-58.89
n$_{(sess.)}$ FAs-allReg	21	49	49	48	48	50	48	49	21	n.a.
n$_{(sess.)}$ FAs-B$_1$	2	17	16	16	17	17	17	17	0	n.a.
n$_{(sess.)}$ FAs-C$_{1,2}$	15	14	15	14	13	15	14	14	15	n.a.
n$_{(sess.)}$ FAs-X	0	12	12	12	12	12	12	12	0	n.a.
n$_{(sess.)}$ FAs-Y	6	6	6	6	6	6	5	6	6	n.a.

<u>Increases</u> in rest during visitation were generally low (highest mean-value: 5 %) and not observed at ***all regimes*** (tab. 5.3.1-15); due to the latter fact, no overall trend is provided.

With respect to ***specific regimes***, increases were limited to one single bird (appendix 5.3.1-1) each at FAs-B$_1$ and X (each for 2 sessions), and four birds of FAs-C$_{1,2}$ (each for 1 session for 1 visiting stage/ 2 consecutive visiting stages). Increases in resting behaviour during human visitation were never observed in FAs-Y.

In 2 of the 3 sessions (appendix 5.3.1-1) for which during-visit resting behaviour was rated the <u>same as pre-visit</u>, resting behaviour had never been predominant prior to visitation; while in the third, predominant resting behaviour had been observed 10-9 min pre-visit only.

Following, **changes in resting behaviour** were examined **in relation to other behaviours**. For this, antidirectional changes ('replacements': decreased resting behaviour coinciding with increases in other behaviour systems and vice versa[17]) as well as syndirectional changes (increases in resting behaviour accompanied by increases in other behavioural systems/ decreases accompanied by other decreases) were investigated during each visiting stage.

Table 5.3.1-16 gives an overview of during-visit <u>antidirectional changes</u>. <u>Decreased</u> resting behaviour was mainly accompanied by increased vigilance (from approach to 15 m until end of visit) and

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[17] N.b.: This table does not provide information on occurrences of increase/ decrease unaccompanied by decreases/ increases in other behaviour systems.

agonistic behaviour (from visitor's stay at 15 m until stay at 3 m). Additionally, 'replacement' by increased breeding behaviour was prominent during the visitor's stays at 5 m and at 3 m as well as during visitor retreat. Increased resting behaviour was rarely observed during the visit; on 12 out of 13 occasions, it occurred in conjunction with decreased vigilance behaviour.

Syndirectional changes (increases in resting behaviour accompanied by increases in other behavioural systems/ decreases accompanied by other decreases) in contrast, were only sporadically observed, except for one session (FA B4-2, 24.11.2000) during which the bird showed reduced resting, comfort and breeding behaviour throughout the visit (appendix 5.3.1-1).

Table 5.3.1-16: During-Visit Changes in Resting Behaviour in Conjunction with Antidirectional Changes in Other Behaviour Systems. For each visiting stage, entries represent numbers of sessions (FAs-allReg) in which a particular conjunction was observed. Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; R: Resting, C: Comfort, B: Breeding, V: Vigilance, A: Agonistic Behaviour; R**+**: increase, R**–**: decrease. **N.b.:** Except for two sessions from FAs-B$_1$, the visiting stages 'along colony – pre' and 'along colony – post' applied only to FAs-C$_{1,2}$ and FAs-Y.

Decreases in Resting Coinciding with Increases in Other Behaviours Systems										**Increases** in Resting Coinciding with Decreases in Other Behaviour systems									
R– coincides with	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post	**R+ coincides with**	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post
C+	o	o	3	1	o	1	o	2	1	**C–**	o	o	o	o	o	o	o	o	o
B+	1	2	3	1	11	4	9	9	3	**B–**	o	1	o	o	o	o	o	o	o
V+	4	24	25	26	36	31	38	30	6	**V–**	o	1	3	3	o	1	o	2	2
A+	o	1	6	5	8	10	13	3	1	**A–**	o	o	o	o	o	o	o	o	o

After the visit (tab. 5.3.1-17), decreases in resting behaviour were still observed far more frequently than increases, although notable (= +17 %) increases did occur.

For ***all regimes*** together, there was a steep drop between the last visiting stage (tab. 5.3.1-15; visitor retreat: -80 %) and the first post-visit interval (1-2 min post-visit: -47 %); afterwards, the proportion of sessions during which decreased resting behaviour was observed declined slowly but steadily to -33 % (9-10 min post-visit).

The mean post-visit value for decreased resting behaviour (-40 %) was approximately two thirds of that obtained during visitation (-63 %), suggesting a response lasting well beyond the visitor's departure.

As for ***specific regimes***, FAs-C$_{1,2}$ and FAs-X showed slight deviations from the pattern outlined above: In FAs-C$_{1,2}$, resting behaviour decreased more during the fourth post-visit interval than during the second and third post-visit intervals. In FAs-X, decreased resting behaviour was less frequent during the first post-visit interval than during the second and third post-visit intervals.

For FAs-B$_1$ and FAs-X, mean post-visit values (-43 %, and -39 %, resp.) for decreased resting behaviour were approximately half those obtained during visitation (-81 %, and -76 %, resp.), while the difference was less pronounced for FAs-C$_{1,2}$ (mean post-visit: -32 % vs. mean during-visit: -54 %) and the smallest change was found for FAs-Y (mean post-visit: -47 % vs. mean during-visit: -59 %).

For ***all regimes*** together, the proportion of sessions for which increases in resting behaviour were observed (i.e., exceeding the 'baseline' of pre-visit behaviour) rose rather steeply (from 8 % to 18 %) between the first and second post-visit interval (1-2 min to 3-4 min post-visit) and subsequently 'oscillated' between approximately +20 % and +25 % for the remainder of the recorded time.

With respect to ***specific regimes***, FAs-C$_{1,2}$ showed increases in resting behaviour immediately during the first post-visit interval (1-2 min post-visit: +19 %), while for FAs-B$_1$ (+23 %) and FAs-X (+25 %), there was a delay of one interval. Concerning FAs-Y, the first increase in resting behaviour was found in the fourth post-visit interval (7-8 min post-visit: +20 %).

The mean post-visit values for increased resting behaviour by far exceeded those found during human visitation in FAs-B$_1$, FAs-C$_{1,2}$, and FAs-X, while FAs-Y had never shown increased resting behaviour during visitation and were late (s.a.) to exhibit it post-visit.

Table 5.3.1-17: Occurrence and Prevalence of Resting Behaviour after Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, **–**: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Resting Behaviour (%)	1-2min post-visit	3-4min post-visit	5-6min post-visit	7-8min post-visit	9-10min post-visit	mean post-visit
FAs-allReg **+**	7.84	18.37	21.74	25.00	19.05	18.40
FAs-B$_1$ **+**	5.88	23.53	25.00	25.00	20.00	19.88
FAs-C$_{1,2}$ **+**	18.75	14.29	21.43	30.77	23.08	21.66
FAs-X **+**	0.00	25.00	16.67	20.00	20.00	16.33
FAs-Y **+**	0.00	0.00	*no %*	20.00	*no %*	6.67
FAs-allReg **–**	-47.06	-42.86	-39.13	-36.36	-33.33	-39.75
FAs-B$_1$ **–**	-52.94	-47.06	-43.75	-37.50	-33.33	-42.92
FAs-C$_{1,2}$ **–**	-50.00	-28.57	-21.43	-38.46	-23.08	-32.31
FAs-X **–**	-33.33	-50.00	-50.00	-30.00	-30.00	-38.67
FAs-Y **–**	-50.00	-50.00	*no %*	-40.00	*no %*	-46.67
n$_{(sess.)}$ FAs-allReg	51	49	46	44	42	n.a.
n$_{(sess.)}$ FAs-B$_1$	17	17	16	16	15	n.a.
n$_{(sess.)}$ FAs-C$_{1,2}$	16	14	14	13	13	n.a.
n$_{(sess.)}$ FAs-X	12	12	12	10	10	n.a.
n$_{(sess.)}$ FAs-Y	6	6	4	5	4	n.a.

In only 4 sessions, post-visit resting behaviour did not differ from pre-visit resting behaviour in any of the intervals (appendix 5.3.1-1). This result was only found for sessions in which pre-visit resting levels had been low: For 3 of these sessions, pre-visit resting behaviour had never been predominant, while for the fourth predominance of resting behaviour had only occurred 10-9 min prior to visitation.

Following, **changes in resting behaviour** were examined **in relation to other behaviour systems**. For this, antidirectional changes (= 'replacements': decreased resting behaviour coinciding with increases in other behaviour systems and vice versa[18]) as well as syndirectional changes (increases in resting behaviour accompanied by increases in other behavioural systems/ decreases accompanied by other decreases) were investigated during each post-visit interval.

Table 5.3.1-18 gives an overview of post-visit antidirectional changes.

Table 5.3.1-18: Post-Visit Changes in Resting Behaviour in Conjunction with Antidirectional Changes in Other Behaviour Systems. For each 2 min-interval, entries represent numbers of sessions in which a particular conjunction was observed (FAs-allReg). Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; min 1-2: 1st Post-visit Interval, comprising the first 2 min after the visit had ended; R: Resting, C: Comfort, B: Breeding, V: Vigilance, A: Agonistic Behaviour; R**+**: increase, R**–**: decrease.

Decreases in Resting Coinciding with Increases in Other Behaviour Systems						**Increases** in Resting Coinciding with Decreases in Other Behaviour Systems					
R– coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10	**R+** coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10
C+	2	3	5	2	1	**C–**	o	1	2	2	1
B+	8	6	10	6	5	**B–**	o	2	2	2	2
V+	20	18	14	11	10	**V–**	2	7	9	9	8
A+	6	2	3	3	1	**A–**	o	o	o	o	o

Decreased resting behaviour was mainly accompanied by increased vigilance and/or breeding behaviour (all intervals). Additionally, 'replacement' by increased agonistic behaviour was prominent during the first post-visit interval (1-2 min), while increased comfort behaviour accounted for a reduction in resting behaviour mainly during the third post-visit interval (5-6 min).

Increased resting behaviour was rarely observed during the first post-visit interval; afterwards, it most often occurred in conjunction with decreased vigilance behaviour (from second post-visit interval to end of records; 3-10 min).

Syndirectional changes (increases in resting behaviour accompanied by increases in other behavioural systems/ decreases accompanied by other decreases) were only sporadically observed.

A decrease in resting behaviour as a response to 'stationary' (i.e., standing/ lying, but not moving) **conspecifics** at the focal nest was observed in 1 of 5 sessions for FAs-B$_1$[19], but not for other FAs (appendix 5.3.1-1). Conspecific movement at the focal nest elicited that response in 2 of 12 sessions (at two different nests of FAs-B$_1$). Reduced resting behaviour during increased conspecific movement (irrespective of distance from the focal nest) was found for 7 sessions in FAs-B$_1$, 1 session each in with respect to FAs-C$_{1,2}$ and FAs-X, and never in FAs-Y (appendix 5.3.1-1).

Skua low overflights coincided with a reduction in resting behaviour in 5 of 13 sessions (1 of 1 for FAs-B$_1$ and FAs-X, 2 of 9 for FAs-C$_{1,2}$, 1 of 2 for FAs-Y; appendix 5.3.1-1). Reduced resting behaviour during skua presence on the ground close to the focal nest was observed for 4 of 5 sessions; and one of the two focal birds concerned showed reduced resting behaviour during **aircraft noise**.

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[18] N.b.: This table does not provide information on occurrences of increase/ decrease unaccompanied by decreases/ increases in other behaviour systems.

[19] In the other sessions recorded at FAs-B$_1$, no conspecific 'stationary' presence had occurred.

For none of these disturbance types, increases in resting behaviour were observed (appendix 5.3.1-1).

5.3.1.5 Comfort Behaviour

Summing up, comfort behaviour was rarely observed prior to visitation (mean FAs-allReg: 11 % = 14 sessions). Due to overall scarcity (appendix 5.3.1-1), results were only calculated for all regimes together. Both increases and decreases (as compared to pre-visit) were observed, with mean decreases being more frequent than mean increases during, but not after visitation (approx. equal).

Comparing disturbance types (human visitation, conspecific disturbance, skua/ aircraft disturbance), comfort behaviour changed in approximately a third of the sessions during **human** visitation, and in approximately half the sessions after visitation. Towards **conspecific**, **skua**, or **aircraft** disturbance, neither increased nor decreased comfort behaviour constituted a consistent reaction.

Comparing visiting stages and post-visit 2 min-intervals, changes after visitation were observed more often than during visitation. During visitation, decreases (mean during-visit: -24 %) were more common than increases (mean during-visit: +8 %), while after visitation, increases and decreases occurred approximately equally often (mean post-visit values: -25 % and +24 %).

The **highest mean-values** for decreased comfort behaviour were found after visitation, in the fourth and third post-visit intervals (7-8min: -33 %; 5-6 min: -31 %), followed by values from ‘approach to 5 m’ through ‘visitor retreat’ during visitation (all -29 %[20]).

With respect to increases, by far the **highest mean-value** was calculated for the third post-visit interval (5-6 min: +46 %).

General findings: Comfort behaviour was observed in approximately one quarter of all sessions analysed (appendix 5.3.1-1), viz., in half of the sessions recorded of FAs-X and FAs-Y (6 of 12 sessions and 3 of 6 sessions, resp.), and much less frequently for FAs-B_1 and FAs-$C_{1,2}$ (2 of 17 sessions and 3 of 16 sessions, resp.). During 1 session each of FAs-$C_{1,2}$ and FAs-Y, comfort behaviour only occurred prior to visitation. In the remaining sessions it did not occur at all.

While table 5.3.1-19 gives an impression of overall scarcity of findings (i.e., values are based on all sessions), only those sessions during which prolonged stretches or repeated occurrences of comfort behaviour had been observed prior to and/or during visitation (14 out of 51) were used for visual appraisal of changes during and after human visitation.

N.b.: Due to said scarcity of occurrence, only overall results on ***all regimes*** together are presented.

Prior to human visitation, comfort behaviour was classified as absent (not shown), occurring or predominant for each interval. Table 5.3.1-19 indicates that absence of comfort behaviour was by far the most common finding for ***all regimes*** and sessions together.

Predominant comfort behaviour was observed in only 2 sessions (appendix 5.3.1-1). In each of these sessions, comfort behaviour entirely replaced resting behaviour for one 2 min-interval.

Longer stretches of occurrence of comfort behaviour within a 2 min-interval, however, were not uncommon.

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[20] A higher value (40 %) based on fewer FAs (5) was calculated for the stage ‘visitor along colony – post’, which applied only to FAs-$C_{1,2}$ and FAs-Y.

Immediately before the visit (2-1 min pre-visit), comfort behaviour was observed in 9 % of all sessions, constituting 25 % of all sessions used for the following appraisal.

Table 5.3.1-19: Occurrence and Predominance of Comfort Behaviour before Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; Occurs: occurring, Predom: predominant, n (sess.): number of sessions proportion is based on; n.a.: not applicable.

Comfort Behaviour (%)	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg **Occurs**	15.63	9.30	13.04	8.16	8.51	10.93
FAs-allReg **Predom**	3.13	0.00	0.00	2.04	0.00	1.03
n$_{(sess.)}$ FAs-allReg	32	43	46	49	47	n.a.

Changes in comfort behaviour were observed throughout **human visitation** (mean during-visit values: -24 % vs. +8 %; tab. 5.3.1-20). Compared to pre-visit behaviour, decreases were more common than increases. Decreases were observed from the visiting stage 'visitor approach to 15 m' onwards throughout the visit[21].

Increases, in contrast, were not found in all visiting stages.

Table 5.3.1-20: Occurrence and Prevalence of Comfort Behaviour during Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, **–**: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable. **N.b.:** Except for two sessions from FAs-B$_1$, the visiting stages 'visitor along colony (20-25 m)' immediately pre-visit and post-visit applied only to FAs-C$_{1,2}$ and FAs-Y.

Comfort Behaviour (%)	**visitor along colony (20-25m)**	**visitor approach to 15m**	**visitor @ 15m**	**visitor approach to 5m**	**visitor @ 5m**	**visitor approach to 3m**	**visitor @ 3m**	**visitor retreat**	**visitor along colony (20-25m)**	**mean during-visit**
FAs-allReg **+**	0.00	0.00	21.43	7.14	0.00	7.14	0.00	14.29	20.00	7.78
FAs-allReg **–**	0.00	-14.29	-21.43	-28.57	-28.57	-28.57	-28.57	-28.57	-40.00	-24.29
n$_{(sess.)}$ FAs-allReg	6	14	14	14	14	14	14	14	5	n.a.

The mean during-visit value for decreased comfort behaviour (-24 %) was substantially higher than that for increased comfort behaviour (+8 %).

A continuing decrease in comfort behaviour occurred in 4 of 14 sessions. A prolonged increase (during several, but not all, stages of the visit) was found in only 1 session, while no change throughout visitation was found in 6 sessions (appendix 5.3.1-1).

After human visitation (tab. 5.3.1-21), there was nearly no difference between the proportions of increases and decreases in comfort behaviour.

The peak value for increases was found in the third post-visit interval (+46 %), while decreases peaked in the fourth post-visit interval (-33 %).

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[21] N.b.: The visiting stages 'visitor along colony' before and after visitation only applied to FAs-C$_{1,2}$ and FAs-Y.

Table 5.3.1-21: Occurrence and Prevalence of Comfort Behaviour <u>after</u> Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, **–**: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable.

Comfort Behaviour (%)	**1-2min post-visit**	**3-4min post-visit**	**5-6min post-visit**	**7-8min post-visit**	**9-10min post-visit**	**mean post-visit**
FAs-allReg **+**	21.43	28.57	46.15	16.67	9.09	24.38
FAs-allReg **–**	-14.29	-21.43	-30.77	-33.33	-27.27	-25.42
n$_{(sess.)}$ FAs-allReg	14	14	13	12	11	n.a.

The <u>mean post-visit value</u> for <u>increased</u> comfort behaviour (+24 %) was approximately three times the mean during-visit value (+8 %), while the respective value for <u>decreased</u> comfort behaviour (-25 %) hardly differed from the during-visit one (-24 %).

As for prolonged changes (appendix 5.3.1-1), a <u>decrease</u> in comfort behaviour persisted (from during-visit into the post-visit period) in 3 sessions, while a continuing <u>increase</u> persisted in 1 session. In a further 3 sessions, focal birds showed increased comfort behaviour <u>only</u> after the human visitor(s) had left.

Changes (increases or decreases) in comfort behaviour were not observed in response to **conspecific** presence/ movement at the focal nest, increased conspecific movement (irrespective of distance from the focal nest), **skua** disturbance or **aircraft** noise.

5.3.1.6 Breeding Behaviour

<u>Summing up</u>, occurrence of breeding behaviour was frequently observed <u>prior to visitation</u> (FAs-allReg mean pre-visit: +41 %). <u>Increases</u> (as compared to pre-visit) constituted the <u>main change</u> observed in breeding behaviour both during (max. during-visit value FAs-allReg: +35 %) and after visitation (max. post-visit value: +31 %). Decreases were rare, and never observed in FAs-C$_{1,2}$ and FAs-Y (appendix 5.3.1-2.05).

<u>Comparing disturbance types</u> (human visitation, conspecific disturbance, skua/ aircraft disturbance; FAs-allReg), breeding behaviour increased rather than decreased both during and after **human** visitation, with mean during-visit values (+16 %) lower than mean post-visit ones (+22 %).

Changes in breeding behaviour did not constitute a consistent reaction towards **conspecifics**, nor were they observed in response to disturbance by **skua on the ground** or **aircraft** noise. **Skua low overflight** elicited increased breeding behaviour in one session at FAs-B$_1$ (out of a total of 13 for all FAs).

<u>Comparing visiting stages and post-visit 2 min-intervals</u> (FAs-allReg), the **highest mean-values** for increased breeding behaviour (+35 % and +31 %, resp.) were found at 5 m distance from the focal animal's nest during visitation, and during the third post-visit interval (5-6 min), respectively. These were followed by values obtained at 3 m distance from the focal animal's nest during visitation (+25 %), in the third post-visit interval (+22 %), during visitor retreat (+21 %), and in the first post-visit interval (1-2 min; also +21 %).

<u>Comparing FAs subjected to different regimes</u>, values for increased breeding behaviour calculated during and after visitation did not continuously single out any of the regimes; the **highest values**

were obtained for FAs-C$_{1,2}$ at visiting stage 'visitor at 5 m' (+60 %), and for FAs-B$_1$ during the third post-visit interval (5-6 min: +50 %).

Both during- and post-visit, FAs from different regimes showed temporal differences with respect to **peak values**. During visitation, peak values for FAs-B$_1$ (+38 %), FAs-C$_{1,2}$ (+60 %), and FAs-Y (+33 %) occurred during the visiting stage 'visitor at 5 m'; for the latter, the same value was obtained again during visitor retreat. After visitation, the peak value for FAs-Y (1-2 min: +33 %) occurred earliest, followed by those from FAs-B$_1$ (+50 %) and FAs-C$_{1,2}$ (+33 %) during the third post-visit interval (5-6 min). In contrast, increased breeding behaviour in FAs-X was not observed until 5-6 min post-visit (+9 %), and 'peaked' during the last post-visit interval included in evaluations (9-10 min: +22 %).

<u>"Curiouser and Curiouser"</u>: For two FAs-B$_1$ and one FA-X, decreases in breeding behaviour were observed both during and after visitation (appendix 5.3.1-1).

General findings: While frequently shown for longer stretches of time within a 2 min-interval, predominant (i.e., exclusively or almost exclusively exhibited) breeding behaviour did not occur in any of the intervals pre-, during-[22] , and post-visit considered here.

N.b.: For visual appraisal of changes during and after human visitation, only sessions during which changes in breeding behaviour had been observed (40 to 42 of 51, depending on stage of visit) were used.

Prior to human visitation, breeding behaviour was classified as either occurring or absent for each interval. Table 5.3.1-22 shows that for ***all regimes*** and all sessions taken together, occurrence of pre-visit breeding behaviour oscillated between 35 % and 46 % (mean pre-visit: 41 %).

<u>Immediately before the visit</u> (2-1 min pre-visit), occurrence was observed in 46 % of all sessions.

The occurrence of pre-visit breeding behaviour differed among ***specific regimes***: Breeding behaviour was encountered most frequently in FAs-C$_{1,2}$ (64 %), and least frequently in FAs-B$_1$ (21 %).

Table 5.3.1-22: Occurrence of Breeding Behaviour <u>before</u> Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; Occurs: occurring; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Breeding Behaviour (%)	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg **Occurs**	40.63	38.10	34.78	44.90	45.83	40.85
FAs-B$_1$ **Occurs**	*no %*	15.38	15.38	35.29	18.75	21.20
FAs-C$_{1,2}$ **Occurs**	70.00	69.23	53.33	50.00	78.57	64.23
FAs-X **Occurs**	41.67	27.27	33.33	58.33	50.00	42.12
FAs-Y **Occurs**	16.67	40.00	33.33	33.33	33.33	31.33
n$_{(sess.)}$ FAs-allReg	32	42	46	49	48	n.a.
n$_{(sess.)}$ FAs-B$_1$	4	13	13	17	16	n.a.
n$_{(sess.)}$ FAs-C$_{1,2}$	10	13	15	14	14	n.a.
n$_{(sess.)}$ FAs-X	12	11	12	12	12	n.a.
n$_{(sess.)}$ FAs-Y	6	5	6	6	6	n.a.

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[22] Predominance during the very short intervals of visitor movement from one distance to the next (lasting << than 2 min) is incomparable in this respect.

Compared to pre-visit behaviour, increases in breeding behaviour (FAs-allReg, range: +5 % to +35 %, mean during-visit: +16 %) were observed far more frequently than decreases **during human visitation** (tab. 5.3.1-23). For ***all regimes*** together, the highest values for increases in breeding behaviour were found when the visitor(s) remained at 5 m distance from the focal nest (+35 %), followed by values obtained for visitor(s) at 3 m distance from the focal nest (+25 %) and during visitor retreat (+22 %).

With respect to ***regime differences***, peak values calculated for FAs-X were lower (max. +18 %) and occurred later than at the other regimes. FAs-$C_{1,2}$ accounted for the highest peak value (+60 %; visitor at 5 m), and were the only ones for which increased breeding behaviour was observed in at least one session for each visiting stage (appendix 5.3.1-1).

The mean during-visit value for increases was highest at FAs-$C_{1,2}$ (+21 %), slightly lower for FAs-B_1 and FAs-Y (both +17 %), and considerably lower (+9 %) for FAs-X.

Decreases were not observed at ***all regimes***; therefore no overall trend is described.

As for ***specific regimes***, breeding behaviour during visits never decreased in FAs-$C_{1,2}$ and FAs-Y, while at FAs-B_1 (2 birds[23]) and X (1 bird[24]) single birds showed reduced breeding behaviour (appendix 5.3.1-1).

Table 5.3.1-23: Occurrence and Prevalence of Breeding Behaviour during Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, **–**: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded. **N.b.:** Except for two sessions from FAs-B_1 (% not shown), the visiting stages 'visitor along colony (20-25 m)' immediately pre-visit and post-visit applied only to FAs-$C_{1,2}$ and FAs-Y.

Breeding Behaviour (%)	**visitor along colony (20-25m)**	**visitor approach to 15m**	**visitor @ 15m**	**visitor approach to 5m**	**visitor @ 5m**	**visitor approach to 3m**	**visitor @ 3m**	**visitor retreat**	**visitor along colony (20-25m)**	**mean during-visit**
FAs-allReg **+**	9.52	4.76	11.90	7.50	35.00	9.52	25.00	21.43	16.67	15.70
FAs-B_1 **+**	*no %*	7.69	0.00	8.33	38.46	15.38	23.08	23.08	n.a.	16.58
FAs-$C_{1,2}$ **+**	7.69	8.33	23.08	9.09	60.00	8.33	36.36	16.67	16.67	20.69
FAs-X **+**	n.a.	0.00	9.09	0.00	9.09	9.09	18.18	18.18	n.a.	9.09
FAs-Y **+**	16.67	0.00	16.67	16.67	33.33	0.00	20.00	33.33	16.67	17.04
FAs-allReg **–**	n.a.	-7.14	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B_1 **–**	*no %*	-15.38	-8.33	-8.33	-15.38	-15.38	-15.38	-15.38	n.a.	-13.37
FAs-$C_{1,2}$ **–**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
FAs-X **–**	n.a.	-9.09	0.00	0.00	-9.09	0.00	-9.09	0.00	n.a.	-3.90
FAs-Y **–**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$n_{(sess.)}$ FAs-allReg	21	42	42	40	40	42	40	42	18	n.a.
$n_{(sess.)}$ FAs-B_1	2	13	12	12	13	13	13	13	0	n.a.
$n_{(sess.)}$ FAs-$C_{1,2}$	13	12	13	11	10	12	11	12	12	n.a.
$n_{(sess.)}$ FAs-X	0	11	11	11	11	11	11	11	0	n.a.
$n_{(sess.)}$ FAs-Y	6	6	6	6	6	6	5	6	6	n.a.

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[23] B3-1 and B4-2, on 24 Nov. 2000 morning

[24] X2-1, on 26 Nov. 2001 morning

After human visitation (tab. 5.3.1-24), increases in breeding behaviour (as compared to pre-visit behaviour) were observed more frequently (mean post-visit: +22 %) than decreases, which did not at all occur in FAs-$C_{1,2}$ and FAs-Y (appendix 5.3.1-2.05).

Looking at ***all regimes*** together, increased breeding behaviour rose during the first 3 post-visit intervals (peak value: +31 %), then waned, until 9-10 min after the visitor had left, increased breeding behaviour was still observed in 19 % of all sessions. The mean post-visit value for increased breeding behaviour (+22 %) was higher than the respective during-visit value (+16 %).

Table 5.3.1-24: Occurrence and Prevalence of Breeding Behaviour after Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, **–**: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Breeding Behaviour (%)	**1-2min post-visit**	**3-4min post-visit**	**5-6min post-visit**	**7-8min post-visit**	**9-10min post-visit**	**mean post-visit**
FAs-allReg **+**	20.93	21.95	30.77	18.92	19.44	22.40
FAs-B_1 **+**	30.77	38.46	50.00	16.67	16.67	30.51
FAs-$C_{1,2}$ **+**	23.08	27.27	33.33	27.27	18.18	25.83
FAs-X **+**	0.00	0.00	9.09	11.11	22.22	8.48
FAs-Y **+**	33.33	16.67	*no %*	20.00	*no %*	23.33
FAs-allReg **–**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B_1 **–**	-7.69	-15.38	-16.67	-16.67	-16.67	-14.62
FAs-$C_{1,2}$ **–**	0.00	0.00	0.00	0.00	0.00	0.00
FAs-X **–**	-9.09	-9.09	0.00	0.00	0.00	-3.64
FAs-Y **–**	0.00	0.00	*no %*	0.00	*no %*	0.00
$n_{(sess.)}$ FAs-allReg	43	41	39	37	36	n.a.
$n_{(sess.)}$ FAs-B_1	13	13	12	12	12	n.a.
$n_{(sess.)}$ FAs-$C_{1,2}$	13	11	12	11	11	n.a.
$n_{(sess.)}$ FAs-X	11	11	11	9	9	n.a.
$n_{(sess.)}$ FAs-Y	6	6	4	5	4	n.a.

As for ***specific regimes***, for FAs-B_1 and FAs-$C_{1,2}$, increases peaked during the third post-visit interval (5-6 min post-visit). With respect to FAs-X, increases in breeding behaviour were not observed during the first two post-visit intervals; values began to rise only from the third post-visit interval onwards (5-10 min) and peaked in the last (at +22 %). As for FAs-Y, increased breeding peaked during the first post-visit interval.

The mean post-visit values were similar for FAs-$C_{1,2}$ and FAs-Y (+26 %, +23 %), higher for FAs-B_1 (+31 %) and substantially lower for FAs-X (+8 %). Compared to mean during-visit values, post-visit increases in breeding behaviour were more pronounced except for FAs-X (mean during-visit: +9 %, mean post-visit: +8 %), and the greatest difference was found for FAs-B_1 (mean during-visit: +17 % vs. mean post-visit: +31 %).

Decreases in breeding behaviour were not observed at ***all regimes***. Concerning ***specific regimes***, decreases persisted for 4 min[25], 8 min, and 10 min[26] (both FAs-B_1, 24.11.2000), respectively, in 3 sessions. Post-visit decreases in breeding behaviour were never observed in FAs-$C_{1,2}$ and FAs-Y (5.3.1-2.05).

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[25] X2-1, on 26 Nov. 2001 morning

[26] B3-1 and B4-2, on 24 Nov. 2000 morning

Mean post-visit values for decreased breeding behaviour in FAs-B_1 and FAs-X hardly differed from mean during-visit values.

No responses in breeding behaviour were found with respect to **conspecific** movement at the focal nest, increased conspecific movement (irrespective of distance from the focal nest), **skua** presence on the **ground** (close to the respective focal nest), or **aircraft noise**.

In the only session from FAs-B_1 in which **skua low overflights** had coincided with breeding behaviour, breeding behaviour increased. At the other three regimes (FAs-$C_{1,2}$: 9 sessions, FAs-X: 1 session, FAs-Y: 2 sessions), no influence of skua low overflight on breeding behaviour was obvious.

5.3.1.7 Vigilance Behaviour

Summing up, occurrence of vigilance behaviour (FAs-allReg mean pre-visit: 76 %) was very frequently observed prior to visitation, whereas predominance of vigilance behaviour was comparatively rare (FAs-allReg mean pre-visit: 14 %). Increases (as compared to pre-visit) constituted the main change observed in vigilance behaviour both during (max. during-visit value FAs-allReg: +81 %) and after visitation (max. post-visit value: +43 %).

Comparing disturbance types (human visitation, conspecific disturbance, skua/ aircraft disturbance; FAs-allReg), vigilance increased in the majority of sessions during **human** visitation, and increases remained prominent post-visit; mean during-visit values (+56 %) were distinctly higher than mean post-visit ones (+34 %).

Increased vigilance did not constitute a consistent reaction towards **conspecifics**, but was observed in 29 % of all sessions in conjunction with increased conspecific movement irrespective of distance from the focal nest. In response to **skua** disturbance, vigilance increased in nearly one-half of all low overflights recorded, while skua presence on the ground invariably elicited that response. **Aircraft** noise likewise invariably resulted in increased vigilance.

Comparing visiting stages and post-visit 2 min-intervals (FAs-allReg), the highest mean-values for increased vigilance (+81 % and +75 %, resp.) were found at 3 m and at 5 m distance from the focal animal’s nest during visitation, followed by values obtained during visitor retreat (+65 %) and approach to 3 m (+64 %). Mean-values for post-visit intervals were substantially lower, with highest values obtained for the second and first post-visit intervals (3-4 min: +43 %; 1-2 min: +41 %).

Antidirectional changes during visitation predominantly concerned resting behaviour in that increased vigilance was accompanied by decreased resting throughout the visit. On a few occasions each, vigilance behaviour ‘replaced’ comfort and breeding behaviour, particularly between ‘approach to 3 m’ and visitor retreat. After visitation, increased vigilance continued to be accompanied by decreased resting behaviour, but this combination was less frequently observed as the post-visit period progressed. During visitation, decreased vigilance behaviour was never prominently associated with increases in other behaviours; after visitation, it was exceedingly frequently ‘replaced’ by increased resting behaviour from the second post-visit interval onwards.

Syndirectional changes were predominantly combinations of increase, i.e., decreased vigilance was not common in the first place and then rarely accompanied by other behaviours decreasing in conjunction. Increased vigilance was most often accompanied by increased occurrence of headshakes, increased posture changes, and increased breeding and agonistic behaviours. During visitation, the visiting stages ‘visitor at 5 m’ and ‘visitor at 3 m’ contained the whole conglomerate, whereas for other visiting stages specific combinations were prominent. After visitation, joint increases were frequently observed up until and including the third post-visit interval (5-6 min), but again, not all combinations showed the same pattern: Increased vigilance in conjunction with increased agonistics was only prominent in the first post-visit interval, while increased posture changes coincided with increased vigilance mostly in the second and third post-visit intervals. Increased vigilance in combination with increased occurrence of headshakes peaked in the first and was still prominent in the two following post-visit intervals, and instances of increased vigilance accompanied by increased breeding behaviour retained a ‘stable prominence’ from first to third post-visit interval.

Comparing FAs subjected to different regimes, values for increased vigilance calculated for FAs-C$_{1,2}$ during visitation frequently reached **lower change classes** than those of the other regimes (all stages following and excluding visitor approach to 15 m). The **highest value** during visitation was obtained from FAs-Y, for visiting stage ‘visitor at 3 m’ (+100 %). During-visit, FAs from different regimes did not differ in position of **peak value** (all during the visiting stage ‘visitor at 3 m’), but with respect to FAs-X, the same value had already been calculated for the stage ‘visitor at 5 m’. Post-visit peak values for FAs-B$_1$, FAs-C$_{1,2}$, and FAs-Y were found in the first post-visit interval (1-2 min), with values for FAs-Y remaining unchanged in the second post-visit interval (3-4 min). For FAs-X, the peak value was calculated for the second post-visit interval.

General findings: Vigilance behaviour was observed in all 51 sessions recorded. An entire absence of vigilance throughout the pre-visit period was never observed, but longer stretches without vigilance behaviour were found in some sessions. Likewise, prolonged vigilance (predominance) showed substantial differences between sessions. For establishment of the pre-visit baseline, the extent to which vigilance behaviour had been predominant/ absent was examined (tab. 5.1.3-26).

Table 5.3.1-25: Occurrence and Predominance of Vigilance Behaviour before Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; Occurs: occurring, Predom: predominant; n (sess.): number of sessions proportion is based on, n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Vigilance Behaviour (%)	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg **Occurs**	78.13	76.19	76.09	77.55	73.47	76.28
FAs-B$_1$ **Occurs**	*no %*	76.92	69.23	70.59	87.50	76.06
FAs-C$_{1,2}$ **Occurs**	70.00	76.92	80.00	71.43	60.00	71.67
FAs-X **Occurs**	91.67	72.73	75.00	100.00	75.00	82.88
FAs-Y **Occurs**	83.33	80.00	83.33	66.67	66.67	76.00
FAs-allReg **Predom**	12.50	11.90	8.70	20.41	14.29	13.56
FAs-B$_1$ **Predom**	*no %*	7.69	15.38	29.41	12.50	16.25
FAs-C$_{1,2}$ **Predom**	30.00	23.08	6.67	28.57	33.33	24.33
FAs-X **Predom**	8.33	9.09	0.00	0.00	0.00	3.48
FAs-Y **Predom**	0.00	0.00	16.67	16.67	0.00	6.67
$n_{(sess.)}$ FAs-allReg	32	42	46	49	49	n.a.
$n_{(sess.)}$ FAs-B$_1$	4	13	13	17	16	n.a.
$n_{(sess.)}$ FAs-C$_{1,2}$	10	13	15	14	15	n.a.
$n_{(sess.)}$ FAs-X	12	11	12	12	12	n.a.
$n_{(sess.)}$ FAs-Y	6	5	6	6	6	n.a.

Before human visitation, vigilance behaviour was classified as predominant, occurring, or entirely absent for each 2 min-interval recorded (tab. 5.1.3-25). Looking at ***all regimes*** together, the class ‘occurring’ comprised between 73 % and 78 % (mean pre-visit: 76 %) of all recordings of each of the 5 pre-visit intervals, while the class ‘predominant’ only contained between 9 % and 20 % (mean pre-visit: 14 %).

Immediately before the visit (2-1 min pre-visit), vigilance was observed to occur in 73 % of all sessions; it was predominant in a further 14 % of all sessions.

As for ***regime differences***, overall pre-visit vigilance (adding values for ‘occurring’ and ‘predominant’) was highest for FAs-C$_{1,2}$ (Σ96 %)[27], and lowest for FAs-Y (Σ83 %). The highest mean value for predominant vigilance behaviour was obtained from FAs-C$_{1,2}$ (24 %). FAs-X brought up the rear in that respect (3 %), while attaining the highest value for occurrence of vigilance (83 %). Mean pre-visit values for occurrence of vigilance were lowest for FAs- C$_{1,2}$ (72 %).

Looking at extent of predominance and absence of vigilance prior to visitation (tab. 5.3.1-26), the categories ‘never predominant’ and ‘never absent’, respectively, attain much greater prominence (67 % and 73 %, resp.) than their respective ‘opposites’ (‘always predominant’: 6 %/ ‘always absent’: 0 %) – indicating that vigilance was always there but rarely continuously sustained for long periods.

Table 5.3.1-26: Consecutive Two-Minute Intervals during which Vigilance Behaviour was Predominant/ Absent before Human Visitation. Values on 5 to 1 intervals are presented cumulatively. Proportions in brackets represent the extent to which vigilance behaviour was always predominant/ absent (100 % = n). FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; V: vigilance; predominant: entirely uninterrupted or with very few and short interruptions; always: in all of the 2 min-intervals of a given session (includes sessions with less than five 2 min-intervals due to data loss); never: during none of the pre-visit intervals recorded in a given session; o: empty category; number of sessions recorded: FAs-allReg = 51, B$_1$ = 17, C$_{1,2}$ = 16, X = 12, Y = 6.

Vigilance predominant	for **5** consecutive intervals	for at least **4** consecutive intervals	for at least **3** consecutive intervals	for at least **2** consecutive intervals	for **1/ disjunct single** intervals	**always** predominant	**never** predominant	**Vigilance absent**	for **5** consecutive intervals	for at least **4** consecutive intervals	for at least **3** consecutive intervals	for at least **2** consecutive intervals	for **1/ disjunct single** intervals	**always** absent	**never** absent
FAs-allReg	o	o	2	10	17	3 (6%)	35 (67%)	FAs-allReg	o	o	o	4	15	o	37 (73%)
FAs-B$_1$	o	o	1	3	6	3 (18%)	11 (65%)	FAs-B$_1$	o	o	o	2	4	o	13 (76%)
FAs-C$_{1,2}$	o	o	1	5	9	o	8 (50%)	FAs-C$_{1,2}$	o	o	o	o	3	o	13 (81%)
FAs-X	o	o	o	1	1	o	11 (92%)	FAs-X	o	o	o	1	5	o	7 (58%)
FAs-Y	o	o	o	1	1	o	5 (83%)	FAs-Y	o	o	o	1	3	o	4 (67%)

Predominance of vigilance behaviour for 6 consecutive minutes (= 3 consecutive intervals) constituted the maximum value within these datasets, and only occurred twice (once each, at FAs-B$_1$ and FAs-C$_{1,2}$)[28]. Stretches of predominant vigilance behaviour for two consecutive intervals were observed in 7 sessions (including one session in which two four-minute stretches were

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[27] N.b.: The symbol Σ is only used to denote ‘sum’.

[28] These are classified as ‘always’ predominant, because for the respective sessions, no more than three pre-visit intervals were available.

observed). In a further 7 sessions, predominant vigilance behaviour was noted for only 1 interval or for disjunct single intervals. Sessions in which vigilance was never predominant were least often encountered in FAs-$C_{1,2}$ (50 %), and most often in FAs-X (92 %).

Absence of vigilance behaviour for 4 consecutive minutes (= 2 consecutive intervals) constituted the maximum value within these datasets, and was observed in 2 sessions from FAs-B_1, in 1 session each for FAs-X and FAs-Y, and never for FAs-$C_{1,2}$. In none of the sessions vigilance behaviour was entirely absent prior to human visitation (FAs-allReg).

During human visitation (tab. 5.3.1-27), an increase in vigilance was observed in the majority of sessions (FAs-allReg; range: +17 % to +81 %, mean during-visit: +56 %). In most sessions, a pronounced increase started as early as during the visitor(s) approach to 15 m, and persisted well into the post-visit period (q.v.).

Looking at ***all regimes***, the highest values for increased vigilance were found when the visitor(s) remained at 3 m (+81 %) and 5 m (+75 %) from the focal nest. In only slightly fewer sessions, increased vigilance during visitor retreat (+65 %) as well as during visitor approach to 3 m (+64 %) was observed.

With respect to ***regime differences***, table 5.3.1-27 shows a slight delay in pronounced responses for FAs-$C_{1,2}$, and a steep early increase (V appr. to 15 m: 83 %) as well as a more continuously high response with respect to FAs-Y.

Table 5.3.1-27: Occurrence and Prevalence of Vigilance Behaviour during Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, **–**: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded. **N.b.:** Except for two sessions from FAs-B_1 (% not shown), the visiting stages 'visitor along colony (20-25 m)' immediately pre-visit and post-visit applied only to FAs-$C_{1,2}$ and FAs-Y.

Vigilance Behaviour (%)	**visitor along colony (20-25m)**	**visitor approach to 15m**	**visitor @ 15m**	**visitor approach to 5m**	**visitor @ 5m**	**visitor approach to 3m**	**visitor @ 3m**	**visitor retreat**	**visitor along colony (20-25m)**	**mean during-visit**
FAs-allReg **+**	17.39	51.02	53.06	58.33	75.00	64.00	81.25	65.31	38.10	55.94
FAs-B_1 **+**	*no%*	58.82	68.75	62.50	88.24	76.47	94.12	82.35	n.a.	75.89
FAs-$C_{1,2}$ **+**	20.00	35.71	26.67	28.57	38.46	46.67	50.00	35.71	33.33	35.01
FAs-X **+**	n.a.	41.67	50.00	83.33	91.67	66.67	91.67	75.00	n.a.	71.43
FAs-Y **+**	16.67	83.33	83.33	66.67	83.33	66.67	100.00	66.67	50.00	68.52
FAs-allReg **–**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B_1 **–**	*no%*	-5.88	-6.25	-6.25	0.00	-5.88	0.00	-5.88	n.a.	-4.31
FAs-$C_{1,2}$ **–**	0.00	0.00	-6.67	-14.29	-15.38	-6.67	-7.14	-7.14	-13.33	-7.85
FAs-X **–**	n.a.	-8.33	-8.33	0.00	0.00	0.00	0.00	0.00	n.a.	-2.38
FAs-Y **–**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$n_{(sess.)}$ FAs-allReg	23	49	49	48	48	50	48	49	21	n.a.
$n_{(sess.)}$ FAs-B_1	2	17	16	16	17	17	17	17	0	n.a.
$n_{(sess.)}$ FAs-$C_{1,2}$	15	14	15	14	13	15	14	14	15	n.a.
$n_{(sess.)}$ FAs-X	0	12	12	12	12	12	12	12	0	n.a.
$n_{(sess.)}$ FAs-Y	6	6	6	6	6	6	5	6	6	n.a.

Table 5.3.1-28: <u>During-Visit</u> Changes in Vigilance Behaviour in Conjunction with Antidirectional Changes in Other Behaviour Systems. For each visiting stage, entries represent numbers of sessions in which a particular conjunction was observed (FAs-allReg). Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; V: Vigilance, R: Resting, C: Comfort, B: Breeding, A: Agonistic Behaviour, H: Headshakes, P: Posture; V**+**: increase, V–: decrease. **N.b.:** Except for two sessions from FAs-B$_1$, the visiting stages ‘along colony – pre’ and ‘along colony – post’ applied only to FAs-C$_{1,2}$ and FAs-Y.

Decreases in Vigilance Coinciding with Increases in Other Behaviour Systems										**Increases** in Vigilance Coinciding with Decreases in Other Behaviour Systems									
V– coincides with	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post	**V+** coincides with	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post
R+	o	1	3	3	o	1	o	2	2	**R–**	4	24	25	26	36	31	38	30	6
C+	o	o	o	o	o	o	o	o	o	**C–**	o	2	2	3	3	4	4	4	2
B+	o	1	o	o	2	1	1	o	o	**B–**	o	2	1	1	2	1	2	2	o
A+	o	o	o	o	1	o	1	o	o	**A–**	o	o	o	o	o	o	o	o	o
H+	o	o	o	o	2	o	1	o	o	**H–**	o	o	o	o	o	o	o	o	o
P+	o	1	o	o	2	o	o	o	o	**P–**	o	o	1	o	1	1	1	1	o

The <u>mean during-visit values</u> were highest for FAs-B$_1$ (+76 %), followed by FAs-X (+71 %) and FAs-Y (+69 %), and considerably lower for FAs-C$_{1,2}$ (+35 %).

<u>Decreases</u> in vigilance did not occur at ***all regimes***; therefore no overall trend is described. As for ***specific regimes***, decreases were never observed for FAs-Y, and never more than once for any given stage (appendix 5.3.1-1) for FAs-B$_1$ (mean: -4 %) and FAs-X (mean: -2 %). With respect to FAs-C$_{1,2}$ (mean: -8 %), they were only slightly more common (tab. 5.3.1-27).

In the 2 sessions for which during-visit vigilance behaviour did <u>not differ from</u> that observed during <u>pre-visit</u> intervals (appendix 5.3.1-1), pre-visit vigilance had been appraised as ‘predominant for at least 2 and 4 intervals, respectively, and as ‘occurring’ for the remaining interval(s).

Following, **changes in vigilance behaviour** were examined **in relation to other behaviours**. For this, antidirectional changes (= ‘replacements’: decreased vigilance behaviour coinciding with increases in other behaviour systems and vice versa[29]) as well as <u>syndirectional changes</u> (increases in vigilance behaviour accompanied by increases in other behavioural systems/ decreases accompanied by other decreases) were investigated during each visiting stage.

Table 5.3.1-28 gives an overview of during-visit <u>antidirectional changes</u>. The vast majority of such ‘replacements’ were observed between <u>increased</u> vigilance and decreased resting behaviour (from approach to 15 m up until the end of the visit). During-visit <u>decreased</u> vigilance was observed far less frequently than increased vigilance, and was rarely accompanied by increases in other

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[29] N.b.: This table does not provide information on occurrences of increase/ decrease unaccompanied by decreases/ increases in other behaviour systems.

behaviours. Of 27 combinations, 12 occurred in conjunction with increased resting behaviour (tab. 5.3.1-28).

In addition, table 5.3.1-29 provides information on syndirectional changes. Decreased vigilance behaviour was rare and very rarely accompanied by decreases in other behaviour systems. In 4 of the 5 combinations encountered, it occurred in conjunction with decreased resting behaviour, suggesting ‘replacement’ of both behaviours by a third.

Increased vigilance most often occurred together with increased headshaking activity, posture changes, and agonistic and breeding behaviour. At the visiting stages ‘visitor at 5 m’ and ‘visitor at 3 m’, the four behaviours and posture changes were jointly observed, whereas at some stages, particular combinations appeared more typical than others: Increased vigilance accompanied by increased occurrence of headshakes became prominent earlier than the other combinations, dominating the stages ‘visitor at 15 m’ and ‘visitor approach to 5 m’. During approach to 3 m, increased vigilance and agonistic behaviours constituted the most frequent combination; while during visitor retreat, increased vigilance was most often accompanied by increased occurrence of headshakes and posture changes.

Table 5.3.1-29: During-Visit Changes in Vigilance Behaviour in Conjunction with Syndirectional Changes in Other Behaviour Systems. For each visiting stage, entries represent numbers of sessions in which a particular conjunction was observed (FAs-allReg). Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; V: Vigilance, R: Resting, C: Comfort, B: Breeding, A: Agonistic Behaviour, H: Headshakes, P: Posture, HR: Heart Rate; V**+**: Increase, V–: Decrease. **N.b.:** Except for two sessions from FAs-B$_1$, the visiting stages ‘along colony – pre’ and ‘along colony – post’ applied only to FAs-C$_{1,2}$ and FAs-Y.

Decreases in Vigilance Coinciding with Decreases in Other Behaviour Systems									**Increases** in Vigilance Coinciding with Increases in Other Behaviour Systems									
V–coincides with	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post	**V+** coincides with	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post
R–	o	1	o	o	1	1	1	o	o	**R+**	o	o	o	o	o	o	o	o	o
C–	o	o	o	o	o	o	o	o	o	**C+**	o	o	2	1	o	1	o	2	o
B–	o	1	o	o	o	o	o	o	o	**B+**	o	o	2	1	9	3	7	4	2
A–	o	o	o	o	o	o	o	o	o	**A+**	o	1	4	3	5	6	10	2	o
H–	o	o	o	o	o	o	o	o	o	**H+**	1	2	6	5	11	3	14	6	o
P–	o	o	o	o	o	o	o	o	o	**P+**	o	3	4	3	12	2	10	5	o

After human visitation (tab. 5.3.1-30), increases in vigilance behaviour as compared to pre-visit remained more frequent than decreases throughout the post-visit period (FAs-allReg, range: +24 % to +43 %; mean post-visit: +34 %). The number of sessions in which increased vigilance was observed declined only gradually. Looking at ***all regimes*** together, values for increased vigilance were approximately equal during the first (+41 %) and second post-visit interval (+43 %), with the latter constituting the post-visit peak value. Increased vigilance continued in 24 % of all sessions as late as 10 min after the visit had ended.

The mean post-visit value for increased vigilance (+34 %) was approximately two thirds of the mean during-visit value (+56 %; tab. 5.3.1-27), suggesting a rather slow waning of response after stimulus removal.

As regards ***specific regimes***, increased vigilance behaviour after visitation was least pronounced for FAs-C$_{1,2}$, and most pronounced for FAs-Y. This was also reflected – for once – in the mean post-visit values: These were highest for FAs-Y (+58 %) followed by FAs-X (+38 %) and FAs-B$_1$ (+33 %), and by far the lowest for FAs-C$_{1,2}$ (+20 %).

With regard to FAs-B$_1$, FAs-C$_{1,2}$ and FAs-X, mean post-visit values for increased vigilance behaviour were approximately half as high as mean during-visit values, while for FAs-Y the drop was far less pronounced (approx. $^4/_5$: +58 % post-visit as compared to +69 % during-visit).

The persisting increase was partly masked by decreases (as compared to pre-visit) in vigilance found in a rising number of sessions (tab. 5.3.1-30). It should be kept in mind that for each post-visit interval, these values represent individual FAs responding diametrically different (some with increased, others with decreased vigilance).

Decreased vigilance did not occur in all regimes; therefore, no overall trend is described. With respect to ***regime differences***, decreases were never observed in FAs-Y (appendix 5.3.1-2.06), while they were fairly common in the other three regimes (post-visit means: -16 % to -20 %).

In those sessions for which post-visit vigilance behaviour did not differ from that observed during pre-visit intervals, pre-visit vigilance had invariably been appraised as at least ‘occurring’ for each interval (appendix 5.3.1-1).

Table 5.3.1-30: Occurrence and Prevalence of Vigilance Behaviour after Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, –: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Vigilance Behaviour (%)	**1-2min post-visit**	**3-4min post-visit**	**5-6min post-visit**	**7-8min post-visit**	**9-10min post-visit**	**mean post-visit**
FAs-allReg **+**	41.18	42.86	34.78	25.00	23.81	33.53
FAs-B$_1$ **+**	52.94	35.29	31.25	25.00	20.00	32.90
FAs-C$_{1,2}$ **+**	25.00	21.43	14.29	23.08	15.38	19.84
FAs-X **+**	33.33	66.67	50.00	20.00	20.00	38.00
FAs-Y **+**	66.67	66.67	*no %*	40.00	*no %*	57.78
FAs-allReg **–**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B$_1$ **–**	-5.88	-11.76	-25.00	-25.00	-20.00	-17.53
FAs-C$_{1,2}$ **–**	-18.75	-14.29	-21.43	-23.08	-23.08	-20.12
FAs-X **–**	0.00	-25.00	-16.67	-20.00	-20.00	-16.33
FAs-Y **–**	0.00	0.00	*no %*	0.00	*no %*	0.00
$n_{(sess.)}$ FAs-allReg	51	49	46	44	42	n.a.
$n_{(sess.)}$ FAs-B$_1$	17	17	16	16	15	n.a.
$n_{(sess.)}$ FAs-C$_{1,2}$	16	14	14	13	13	n.a.
$n_{(sess.)}$ FAs-X	12	12	12	10	10	n.a.
$n_{(sess.)}$ FAs-Y	6	6	4	5	4	n.a.

Following, **changes in vigilance behaviour** were examined **in relation to other behaviours** (antidirectional/ syndirectional changes[30]). Table 5.3.1-31 gives an overview of post-visit antidirectional changes.

Table 5.3.1-31: Post-Visit Changes in Vigilance Behaviour in Conjunction with Antidirectional Changes in Other Behaviour Systems. For each 2 min-interval, entries represent numbers of sessions in which a particular conjunction was observed (FAs-allReg). Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; min 1-2: 1st Post-visit Interval, comprising the first 2 min after the visit had ended; V: Vigilance, R: Resting, C: Comfort, B: Breeding, A: Agonistic Behaviour; H: Headshakes, P: Posture; V+: increase, V–: decrease.

Decreases in Vigilance Coinciding with Increases in Other Behaviour Systems						**Increases** in Vigilance Coinciding with Decreases in Other Behaviour Systems					
V– coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10	**V+** coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10
R+	2	7	9	9	8	**R–**	20	18	14	11	10
C+	o	o	o	o	o	**C–**	1	1	1	o	o
B+	1	1	o	o	o	**B–**	1	1	o	o	o
A+	o	o	1	o	o	**A–**	o	o	o	o	o
H+	1	o	o	o	o	**H–**	o	o	o	o	o
P+	1	o	o	o	o	**P–**	o	o	o	o	o

The vast majority of such ‘replacements’ were observed between vigilance and resting behaviour. Whereas the first post-visit interval was characterised by few pairs of V-R+ (2 vs. 20 pairs for V+R-), this combination attained near equality with its reverse during the fourth and fifth post-visit intervals (9 vs. 11, and 8 vs. 10 pairs, resp.). If the entire post-visit period is considered, however, the combination V+R- was found approximately twice as often as the opposite conjunction.

In addition, table 5.3.1-32 provides information on syndirectional changes.

Table 5.3.1-32: Post-Visit Changes in Vigilance Behaviour in Conjunction with Syndirectional Changes in Other Behaviour Systems. For each 2 min-interval, entries represent numbers of sessions in which a particular conjunction was observed (FAs-allReg). Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; min 1-2: 1st Post-visit Interval, comprising the fist 2 min after the visit had ended; V: Vigilance, R: Resting, C: Comfort, B: Breeding, A: Agonistic Behaviour, H: Headshakes, P: Posture; V+: increase, V–: decrease.

Decreases in Vigilance coinciding with Decreases in other behaviours						**Increases** in Vigilance coinciding with Increases in other behaviours					
V– coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10	**V+** coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10
R–	1	o	o	o	o	**R+**	o	o	1	o	o
C–	o	o	1	1	1	**C+**	2	2	4	1	o
B–	o	1	2	2	2	**B+**	7	5	7	3	2
A–	o	o	o	o	o	**A+**	5	2	2	2	1
H–	o	o	o	o	o	**H+**	13	7	9	4	2
P–	o	o	1	1	1	**P+**	3	6	7	3	2

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[30] N.b.: This table does not provide information on occurrences of increase/ decrease unaccompanied by decreases/ increases in other behaviour systems.

Decreased vigilance behaviour was rarely accompanied by syndirectional changes in other behaviour systems. In 7 of 14 combinations counted, it occurred in conjunction with decreased breeding behaviour. In the first three post-visit intervals, increased vigilance most often occurred together with increased headshaking activity, breeding, agonistic behaviours (first post-visit interval only), and posture changes. In the last two post-visit intervals, no particular combination attained prominence.

Data on **conspecific** 'stationary' presence at the focal nest did not indicate a clear vigilance response. Conspecific movement at the focal nest elicited increased vigilance in 3 sessions from 3 different focal animals on different dates from FAs-B_1 (appendix 5.3.1-2.06), but not from other FAs. In contrast, increased conspecific movement (irrespective of distance from the focal nest) coincided with increased vigilance in a total of 15 sessions (29 %), and was observed at least once in each of the regimes (appendix 5.3.1-1).

During **skua** low overflights, vigilance increased in approximately half of the sessions (46 %), while the scarce recordings of skua disturbance on the ground (close to the respective focal nest) as well as **aircraft noise** invariably resulted in increased vigilance (skua ground: 5 of 5, aircraft noise: 3 of 3).

Decreases in vigilance as a response to these disturbance types were never observed.

5.3.1.8 Agonistic Behaviour

Summing up, agonistic behaviour was frequently observed prior to visitation (FAs-allReg mean pre-visit: 36 %). Increases constituted the main change observed in agonistic behaviour both during (max. during-visit value FAs-allReg: +33 %) and after visitation (max. post-visit value: +19 %).

Comparing disturbance types (human visitation, conspecific disturbance, skua/ aircraft disturbance; FAs-allReg), increased agonistic behaviour was found both during and after **human** visitation, with mean during-visit values (+16 %) equal[31] to mean post-visit ones (+15 %).

Increased agonistic behaviour constituted a common response towards **conspecific** movement at the focal nest, but was not consistently observed with respect to conspecific 'stationary' presence at the nest, nor conspecific movement irrespective of distance from focal nest. While **'aerial' disturbance** (skua low overflights/ aircraft noise) did not elicit increased agonistic behaviour, **skua** presence on the **ground** near the focal nest resulted in increased agonistic behaviour in 3 out of 4 sessions.

Comparing visiting stages and post-visit 2 min-intervals (FAs-allReg), the **highest mean-values** for increased agonistic behaviour (+33 % and +29 %, resp.) during visitation were found at 3 m distance from the focal animal's nest and during approach to that distance. They were followed by values obtained while the visitor(s) remained at 5 m distance from the focal nest (+21 %), and during the first (1-2 min; +19 %) post-visit interval. Values obtained during visitor approach to 5 m were very similar to the latter (+18 %), while visitor retreat – unlike for other behaviour systems – did not elicit a strong agonistic response (+7%).

Comparing FAs subjected to different regimes, values for increased agonistic behaviour during visitation calculated for FAs-$C_{1,2}$ were frequently higher than for those of the other regimes; the **highest value** was obtained for visiting stage 'visitor at 3 m' at FAs -Y (+60 %).

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[31] differences due to rounding-off error: during-visit: 15.80 % vs. post-visit: 15.48 %

During visitation, FAs-C$_{1,2}$ (+38 %) and FAs-Y (+60 %) had their respective **peak values** during the visiting stage ‘visitor at 3 m’, while FAs-X (+44 %) already peaked during approach to that distance. Peak values for FAs-B$_1$ (+25 %) appeared as early as the stage ‘visitor at 5 m’, and remained elevated until (and excluding) visitor retreat.

Post-visit, FAs from different regimes showed temporal differences with respect to peak values: Peak values occurred in the first post-visit interval with respect to FAs-Y (+33 %), during the second for FAs-C$_{1,2}$ (+31 %), and during the fourth for FAs-B$_1$ (+27 %). Values obtained from FAs-X did not peak at all.

General findings: Agonistic behaviour was not observed in all sessions. Sessions were excluded from appraisal, if agonistic behaviour had not been shown throughout the session (7 sessions), or if agonistic behaviour had been exclusively exhibited before the beginning of the visit (2 sessions). A decrease (as opposed to non-occurrence) in agonistic behaviour as compared to pre-visit behaviour was never observed (appendix 5.3.1-1). Likewise, agonistic behaviour was never predominant.

Prior to human visitation, agonistic behaviour was classified as either occurring or entirely absent (not shown) for each 2 min-interval recorded. For ***all regimes*** together, occurrence of agonistic behaviour ranged from 26 % to 47 % (mean pre-visit: 36 %; tab. 5.3.1-33).

Immediately before the visit (2-1 min pre-visit), occurrence of agonistic behaviour was observed in 40 % of all sessions.

Prior to visitation, differences among ***specific regimes*** were as follows: Occurrence of agonistic behaviour was most frequently encountered in FAs-C$_{1,2}$ (mean pre-visit: 46 %, range: 31 % to 62 %), and least frequently in FAs-Y (mean pre-visit: 28 %, range: 17 % to 40 %). ‘Outliers’ starkly different from other values were observed for FAs-B$_1$ (‘outlier’: 8 %; range 23 % to 53 %; pre-visit mean: 29 %), and FAs-X, (‘outlier’: 58 %; range: 25 % to 33 %; pre-visit mean: 34 %).

During human visitation, agonistic behaviour increased (tab. 5.3.1-34) or remained unchanged[32] , but never decreased as compared to pre-visit levels.

Table 5.3.1-33: Occurrence of Agonistic Behaviour before Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; Occurs: occurring; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Agonistic Behaviour (%)	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg **Occurs**	46.88	28.57	26.09	36.73	40.43	35.74
FAs-B$_1$ **Occurs**	*no %*	23.08	7.69	52.94	31.25	28.74
FAs-C$_{1,2}$ **Occurs**	60.00	30.77	40.00	35.71	61.54	45.60
FAs-X **Occurs**	58.33	27.27	25.00	25.00	33.33	33.79
FAs-Y **Occurs**	16.67	40.00	33.33	16.67	33.33	28.00
$n_{(sess.)}$ FAs-allReg	32	42	46	49	47	n.a.
$n_{(sess.)}$ FAs-B$_1$	4	13	13	17	16	n.a.
$n_{(sess.)}$ FAs-C$_{1,2}$	10	13	15	14	13	n.a.
$n_{(sess.)}$ FAs-X	12	11	12	12	12	n.a.
$n_{(sess.)}$ FAs-Y	6	5	6	6	6	n.a.

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[32] subtract values of tab. 5.3.1-34 from 100 %

Looking at ***all regimes***, increases in agonistic behaviour ranged from +2 % to +33 % (mean during-visit FAs-allReg: +16 %). They steeply rose from +2 % (visitor approach to 15 m) to +17 % (visitor at 15 m) at the beginning of human visitation, and continued to rise as the visit progressed. The highest values for increases in agonistic behaviour were obtained when the visitor(s) remained at 3 m distance from the focal nest (+33 %) and during visitor approach to that distance (+29 %).

As for ***specific regimes***, in FAs-C$_{1,2}$ the increase in agonistic behaviour started earlier (visitor approach to 15 m) than at the other three regimes (visitor at 15 m), and persisted until the end of visitation. For FAs-X, the value during visitor approach to 3 m was higher than while the visitors remained (standing) at 3 m. With respect to FAs-B$_1$, values for increased agonistics rose to +25 % as the visitor stayed at 5 m, and remained at that value up until (and excluding) the stage of visitor retreat. The strongest increase was obtained from FAs-Y between the visitors' approach to 3 m (+17 %) and their staying there (+60 %).

The mean during-visit values were approximately equal (between +14 % and +16 %) for FAs-B$_1$, FAs-X, and FAs-Y, and higher for FAs-C$_{1,2}$ (+21 %).

Table 5.3.1-34: Occurrence and Prevalence of Agonistic Behaviour during Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, –: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded. **N.b.:** Except for two sessions from FAs-B$_1$ (% not shown), the visiting stages 'visitor along colony (20-25 m)' immediately pre-visit and post-visit applied only to FAs-C$_{1,2}$ and FAs-Y.

Agonistic Behaviour (%)	**visitor along colony (20-25m)**	**visitor approach to 15m**	**visitor @ 15m**	**visitor approach to 5m**	**visitor @ 5m**	**visitor approach to 3m**	**visitor @ 3m**	**visitor retreat**	**visitor along colony (20-25m)**	**mean during-visit**
FAs-allReg **+**	4.35	2.44	17.07	17.95	20.51	29.27	33.33	7.32	10.00	15.80
FAs-B$_1$ **+**	*no %*	0.00	9.09	9.09	25.00	25.00	25.00	8.33	n.a.	14.50
FAs-C$_{1,2}$ **+**	0.00	7.14	26.67	23.08	33.33	28.57	38.46	14.29	14.29	20.65
FAs-X **+**	n.a.	0.00	11.11	11.11	11.11	44.44	22.22	0.00	n.a.	14.29
FAs-Y **+**	16.67	0.00	16.67	33.33	0.00	16.67	60.00	0.00	0.00	15.93
n$_{(sess.)}$ FAs-allReg	23	41	41	39	39	41	39	41	20	n.a.
n$_{(sess.)}$ FAs-B$_1$	2	12	11	11	12	12	12	12	0	n.a.
n$_{(sess.)}$ FAs-C$_{1,2}$	15	14	15	13	12	14	13	14	14	n.a.
n$_{(sess.)}$ FAs-X	0	9	9	9	9	9	9	9	0	n.a.
n$_{(sess.)}$ FAs-Y	6	6	6	6	6	6	5	6	6	n.a.

After the visit (tab. 5.3.1-35), values for increased agonistic activity fluctuated between +11 % and +19 % for ***all regimes*** together. Across these fluctuations, occurrence of increased agonistic behaviour (as compared to pre-visit) appeared to wane gradually; and the lowest value was found in the last post-visit interval.

The mean post-visit value for increased agonistic behaviour (+15 %) was approximately equal to that obtained during visitation (+16 %), indicating a tendency for persistence of increased agonistic activities after the visit had ended.

With respect to ***specific regimes***, not all regimes showed increased agonistic activity in all of the post-visit intervals. For FAs-B$_1$, agonistic increase was low during the first and non-existent during the second post-visit intervals, and more pronounced during the remaining intervals. Concerning FAs-X, no increases were observed during the fourth and fifth post-visit intervals. The most pronounced increases[33] were encountered for FAs-Y during the first post-visit interval (+33 %) and for FAs-$C_{1,2}$ during the second post-visit interval (+31 %).

The mean post-visit values were similar for FAs-B_1, FAs-$C_{1,2}$ and FAs-Y (between +15 % and +19 %), and lowest for FAs-X (+11 %). They hardly differed from mean during-visit values.

Table 5.3.1-35: Occurrence and Prevalence of Agonistic Behaviour after Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Agonistic Behaviour (%)	1-2min post-visit	3-4min post-visit	5-6min post-visit	7-8min post-visit	9-10min post-visit	mean post-visit
FAs-allReg **+**	19.05	15.00	18.42	13.51	11.43	15.48
FAs-B_1 **+**	8.33	0.00	18.18	27.27	20.00	14.76
FAs-$C_{1,2}$ **+**	20.00	30.77	21.43	15.38	7.69	19.05
FAs-X **+**	22.22	11.11	22.22	0.00	0.00	11.11
FAs-Y **+**	33.33	16.67	*no %*	0.00	*no %*	16.67
$n_{(sess.)}$ FAs-allReg	42	40	38	37	35	n.a.
$n_{(sess.)}$ FAs-B_1	12	12	11	11	10	n.a.
$n_{(sess.)}$ FAs-$C_{1,2}$	15	13	14	13	13	n.a.
$n_{(sess.)}$ FAs-X	9	9	9	8	8	n.a.
$n_{(sess.)}$ FAs-Y	6	6	4	5	4	n.a.

Increased agonistic behaviour as a response to **conspecific** ‘stationary’ presence at the focal nest was observed during 1 session each of FAs-B_1, FAs-$C_{1,2}$ and FAs-Y, but not for FAs-X (appendix 5.3.1-2.07). As a response to conspecific movement at the focal nest, it was common at ***all regimes*** (FAs-allReg: 48 % of 40 sessions, ranging from 36 % for FAs-B_1 to 60 % for FAs-Y).

In only 3 of 13 sessions from FAs-B_1, increased **conspecific** movement (irrespective of distance from the focal nest) elicited an increase in agonistic behaviour; this was not observed in FAs of other regimes. **Skua low overflights** and **aircraft noise** were not observed to incite an increase in agonistic behaviour, whereas **skua presence on the ground** (close to the focal nest) led to an increase in 3 out of 4 sessions (appendix 5.3.1-2.07).

For these disturbance types, decreases in agonistic behaviour were never observed.

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[33] While 33 % comprised 2 of 6 FAs at group Y, 31 % contained 4 of 13 FAs at group C.

5.3.1.9 Shakes (and the Absence of Displays)

N.b.: By right of intention, this section should have been titled ‘Shakes and Displays’.

Displays, however, were only observed in a few sessions, and *well before visitation* commenced. Besides stating that <u>*with respect to the focal animals examined, displays did not constitute an indicator for human disturbance*</u> as ‘never the twain did meet’, this parameter is thus not mentioned any further (but see discussion).

Concerning the different types of **shakes**, headshakes were by far the most commonly observed type. In the following presentation, the *term headshake* is used generically and *includes ruffle-shakes* – in which, after all, the head is also shaken.

<u>**Summing up**</u>, occurrence of headshakes was infrequently observed <u>prior to visitation</u> (FAs-allReg mean pre-visit: 17 %). <u>Increases</u> in occurrence of headshakes constituted the <u>main change</u> both during (max. value FAs-allReg: +44 %) and after visitation (max. post-visit value: +44 %).

<u>Comparing disturbance types</u> (human visitation, conspecific disturbance, skua/ aircraft disturbance; FAs-allReg), increased occurrence of headshakes was found both during and after **human** visitation, with mean during-visit values (+21 %) lower than mean post-visit ones (+29 %).

Increased occurrence of headshakes did not constitute a consistent reaction towards **conspecifics**. It was rarely observed in response to **skua** low overflight (2 out of 13 sessions), and never to skua presence on the ground or **aircraft** noise.

<u>Comparing visiting stages and post-visit 2 min-intervals</u> (FAs-allReg), the **highest mean-values** for increased occurrence of headshakes (both +44%) were found at 3 m distance from the focal animal’s nest during visitation and in the first post-visit interval (1-2 min), followed by values obtained for the visiting stage ‘visitor at 5 m’ (+38 %), values during the third post-visit interval (5-6 min min; +33 %), and at 15 m distance from the focal nest (+30 %).

<u>Comparing FAs subjected to different regimes</u>, the **highest value** for increased occurrence of headshakes was obtained for FAs-$C_{1,2}$ (‘visitor at 3 m’: +79 %). During visitation, FAs subjected to different regimes showed temporal differences with respect to **peak values**. Increased occurrence of headshakes showed two peaks with respect to FAs-Y (+50 %; at 15 m, and during retreat), peaked during the stage ‘visitor at 5 m’ for FAs-B_1 (+38 %), during the stage ‘visitor at 3 m’ for FAs-$C_{1,2}$ (+79 %), and only during retreat for FAs-X (+36 %).

After visitation, the respective peak values of FAs-$C_{1,2}$, FAs-X, and FAs-Y all occurred in the first post-visit interval (1-2 min), while values for FAs-B_1 peaked in the third post-visit interval (5-6 min).

<u>“Curiouser and Curiouser”</u>: With respect to the penguins examined, displays did not constitute an indicator for human disturbance as ‘never the twain did meet’.

General findings: Complete absence of headshakes (entire session) was more often observed in FAs-B_1 (4 of 17 sessions) than in the other FAs (FAs-$C_{1,2}$: 1 of 16; FAs-X: 1 of 12; FAs-Y: 0 of 6). A <u>decrease</u> in occurrence of headshakes as compared to pre-visit values was <u>never noted</u> (appendix 5.3.1-1).

Only sessions during which headshakes had been observed (45 of 51) were used for visual appraisal.

Prior to human visitation, headshakes were classified as either occurring or absent (not shown) for each 2 min-interval recorded. Looking at ***all regimes*** together, occurrence of headshakes ranged from 12 % to 28 % (mean pre-visit FAs-AllReg: 17 %; tab. 5.3.1-36).

Immediately before the visit (2-1 min pre-visit), occurrence of headshakes was observed in 17 % of all sessions.

As for ***specific regimes***, the lowest values (0 % for 2 single intervals) for 'occurrence' of headshakes were calculated for FAs-B$_1$ (mean pre-visit: 5 %) and FAs-Y (mean pre-visit: 13 %), and the highest for FAs-C$_{1,2}$ (max.: 40 %; mean pre-visit: 28 %).

Table 5.3.1-36: Occurrence of Headshakes before Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; Occur: occurring; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Headshakes (%)	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg **Occur**	28.13	14.29	14.89	12.24	16.67	17.24
FAs-B$_1$ **Occur**	*no %*	0.00	0.00	11.76	6.25	4.50
FAs-C$_{1,2}$ **Occur**	40.00	38.46	25.00	14.29	21.43	27.84
FAs-X **Occur**	33.33	9.09	16.67	16.67	16.67	18.48
FAs-Y **Occur**	16.67	0.00	16.67	0.00	33.33	13.33
n$_{(sess.)}$ FAs-allReg	32	42	47	49	48	n.a.
n$_{(sess.)}$ FAs-B$_1$	4	13	13	17	16	n.a.
n$_{(sess.)}$ FAs-C$_{1,2}$	10	13	16	14	14	n.a.
n$_{(sess.)}$ FAs-X	12	11	12	12	12	n.a.
n$_{(sess.)}$ FAs-Y	6	5	6	6	6	n.a.

During human visitation (tab. 5.3.1-37), increased occurrence of headshakes ranged from +5 % to +44 % (mean during-visit: +21 %). Looking at ***all regimes***, the highest values for increased occurrence of headshakes were found during the visitor(s) stay at 3 m (+44 %), at 5 m from the focal nest (+38 %), and at 15 m (+30 %), respectively. Prominently increased occurrence of headshakes started with the visiting stage 'visitor at 15 m' (+30 % vs. 'visitor approach to 15m': +5%). During retreat, increased occurrence of headshakes was still found in 23 % of all sessions.

N.b.: It should be kept in mind that headshakes represent behavioural events, rather than states, so that 'probability of occurrence' during the much shorter approaches was inevitably lower than during visitor stay at any given distance.

Table 5.3.1.37 shows ***regime differences*** in the position of **peak values** for increased occurrence of headshakes during the visit: For FAs-Y, peak values were calculated first during visitor stay at 15 m, and again during visitor retreat (both +50 %). Those calculated for FAs-B$_1$ reached their peak (+38 %) during visitor stay at 5 m, for FAs-C$_{1,2}$, the peak value (+79 %) occurred at the visiting stage 'visitor at 3 m', while the response of FAs-X did not peak until visitor retreat (+36 %).

The mean during-visit values were lowest for FAs-B$_1$ (+14 %), followed by FAs-X (+21 %), and highest for FAs-C$_{1,2}$ and FAs-Y (+27 % and +29 %, resp.).

Immediately **after the visit** (tab. 5.3.1-38), an increased occurrence of headshakes (as compared to pre-visit values) was observed considerably more often than during visitor retreat[34] , with the

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[34] as well as – concerning groups FAs-C$_{1,2}$ and FAs-Y – during the visiting stage 'visitor along colony – post-visit'

value for ***all regimes*** being equal to that found during the stage of ‘visitor(s) at 3m’ (‘visitor at 3 m = 1-2 min post-visit = +44 %). In the second post-visit interval, it dropped steeply (to +30 %). Increased occurrence of headshakes remained approximately equal between the second and third (+33 %) post-visit intervals, and continued to wane more gradually (+24 %; +17 %) during the last 2 post-visit intervals.

The mean post-visit value for increased occurrence of headshakes (+29 %) was higher than that obtained during visitation (+21 %), and in 17 % of all sessions, an increased occurrence of headshakes (as compared to pre-visit behaviour) was still observed 9-10 min after human visitation.

Table 5.3.1-37: Occurrence and Prevalence of Headshakes during Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded. **N.b.:** Except for two sessions from FAs-B_1 (% not shown), the visiting stages ‘visitor along colony (20-25 m)’ immediately pre-visit and post-visit applied only to FAs-$C_{1,2}$ and FAs-Y.

Headshakes (%)	**visitor along colony (20-25m)**	**visitor approach to 15m**	**visitor @ 15m**	**visitor approach to 5m**	**visitor @ 5m**	**visitor approach to 3m**	**visitor @ 3m**	**visitor retreat**	**visitor along colony (20-25m)**	**mean during-visit**
FAs-allReg **+**	14.29	4.65	30.23	14.29	38.10	13.64	44.19	23.26	10.00	21.40
FAs-B_1 **+**	*no %*	7.69	8.33	8.33	38.46	0.00	30.77	7.69	n.a.	14.47
FAs-$C_{1,2}$ **+**	14.29	0.00	50.00	0.00	50.00	21.43	78.57	15.38	14.29	27.11
FAs-X **+**	n.a.	9.09	18.18	27.27	27.27	9.09	18.18	36.36	n.a.	20.78
FAs-Y **+**	16.67	0.00	50.00	33.33	33.33	33.33	40.00	50.00	0.00	28.52
$n_{(sess.)}$ FAs-allReg	21	43	43	42	42	44	43	43	20	n.a.
$n_{(sess.)}$ FAs-B_1	1	13	12	12	13	13	13	13	0	n.a.
$n_{(sess.)}$ FAs-$C_{1,2}$	14	13	14	13	12	14	14	13	14	n.a.
$n_{(sess.)}$ FAs-X	0	11	11	11	11	11	11	11	0	n.a.
$n_{(sess.)}$ FAs-Y	6	6	6	6	6	6	5	6	6	n.a.

Table 5.3.1-38: Occurrence and Prevalence of Headshakes after Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Headshakes (%)	**1-2min post-visit**	**3-4min post-visit**	**5-6min post-visit**	**7-8min post-visit**	**9-10min post-visit**	**mean post-visit**
FAs-allReg **+**	44.44	29.55	32.50	23.68	16.67	29.37
FAs-B_1 **+**	30.77	30.77	41.67	25.00	18.18	29.28
FAs-$C_{1,2}$ **+**	53.33	35.71	30.77	25.00	16.67	32.30
FAs-X **+**	45.45	18.18	18.18	22.22	11.11	23.03
FAs-Y **+**	50.00	33.33	*no %*	20.00	*no %*	34.44
$n_{(sess.)}$ FAs-allReg	45	44	40	38	36	n.a.
$n_{(sess.)}$ FAs-B_1	13	13	12	12	11	n.a.
$n_{(sess.)}$ FAs-$C_{1,2}$	15	14	13	12	12	n.a.
$n_{(sess.)}$ FAs-X	11	11	11	9	9	n.a.
$n_{(sess.)}$ FAs-Y	6	6	4	5	4	n.a.

As for ***regime differences***, the overall pattern described above represented FAs-$C_{1,2}$, FAs-X, and FAs-Y fairly accurately, while the value for occurrence of headshakes for FAs-B_1 was constant during the first two post-visit intervals (both +31 %), and peaked 5-6 min post-visit (+42 %). For each regime, the lowest value for increased occurrence of headshakes was found in the last post-visit interval.

The <u>mean post-visit values</u> were by far the lowest for FAs-X (+23 %), followed by those obtained from FAs-B_1 (+29 %) and FAs-$C_{1,2}$ (+32 %), and still slightly higher for FAs-Y (+34 %), and. While mean post-visit values were higher than the respective during-visit means for all regimes, the value obtained from FAs-B_1 more than doubled (mean during-visit: +14 % vs. mean post-visit: +29 %).

<u>Increased</u> occurrence of headshakes was neither observed as a response to **conspecific** ‘stationary’ presence nor to increased conspecific movement at the focal nest or irrespective of distance from the focal nest. In 2 out of 13 sessions, occurrence of headshakes increased during **skua** low overflights. No increased occurrence of headshakes was found during the scarce recordings of skua presence on the ground (close to the focal nest) or **aircraft** noise.

For these disturbance types, <u>decreases</u> in occurrence of headshakes were never observed.

5.3.1.10 Posture Changes

<u>Summing up</u>, posture changes were rarely observed <u>prior to visitation</u> (FAs-allReg mean pre-visit: 12 %). <u>Increases</u> in occurrence of posture changes constituted the <u>main change</u> both during (max. during-visit value FAs-allReg: +39 %) and after visitation (max. post-visit value: +28 %).

<u>Comparing disturbance types</u> (human visitation, conspecific disturbance, skua/ aircraft disturbance; FAs-allReg), increased occurrence of posture changes was found both during and after **human visitation**, with mean during-visit values (+17 %) slightly lower than mean post-visit ones (+19 %).

Increased occurrence of posture changes did not constitute a consistent reaction towards **conspecifics**. It was extremely rarely observed in response to **skua** low overflight (1 out of 14 sessions), and never to skua presence on the ground or **aircraft** noise.

<u>Comparing visiting stages and post-visit 2 min-intervals</u> (FAs-allReg), the **highest mean-values** for increased occurrence of posture changes (+39 %, +28 %, and +27 %, resp.) were found at 5 m distance from the focal animal’s nest during visitation, in the third post-visit interval (5-6 min), and during the visitor(s) stay at 3 m. Values obtained during visitor retreat (+23 %) equalled those calculated for the second post-visit interval (3-4 min).

<u>Comparing FAs subjected to different regimes</u>, values for increased occurrence of posture changes during visitation calculated for FAs-$C_{1,2}$ showed more of a continuous elevation than those of the other regimes, which tended to fluctuate more strongly, dropping markedly during approaches to 5 m and 3 m, respectively. The **highest values** were obtained from FAs-B_1, during visitor stay at 5 m as well as during the third post-visit interval (both +43 %).

During visitation, distinct **peak values** occurred during the visiting stage ‘visitor at 5 m’ for FAs-B_1 and FAs-$C_{1,2}$, while two or more visiting stages held equally high values with respect to FAs- X (at 5 m, retreat) and FAs-Y (at 15 m, 5 m, 3 m, retreat).

Post-visit peak values calculated for FAs of different regimes showed temporal differences: Those for FAs-Y lay in the second post-visit interval (3-4 min), for FAs-B$_1$ and FAs-C$_{1,2}$ in the third post-visit interval (5-6 min), and those for FAs-X in the fourth post-visit interval (7-8 min).

<u>“Curiouser and Curiouser”</u>: Decreases in occurrence of posture changes were only observed on one day, and could invariably be attributed to the fact that the two focal animals concerned had been engaged in frequent posture changes prior to visitation. With respect to climatic influence, however, it should be noted that the third FA recorded on that day (C2-2) did not exhibit the same pattern (appendix 5.3.1-1).

General findings: As all focal birds were incubating, the predominant posture exhibited prior to visitation was the prone one (lying on the nest). An upright posture (‘up’, i.e., sitting or standing) was sometimes adopted for longer stretches of time during bouts of nest manipulation (stone rearrangement, gathering of stones in the immediate vicinity of the nest), usually during egg manipulation, and most often, when the bird was preening. During agonistic behaviour, the bird might get up briefly to extend their reach beyond the territory boundaries. The latter accounted for part of the posture changes mentioned below. Additionally, shorter stretches of an upright posture were also observed when the bird repeatedly failed to rearrange the eggs to their satisfaction.

Only sessions during which *changes* in posture had been observed (44 out of 51) were examined for visual appraisal (prone throughout: 7 sessions).

Prior to human visitation, posture changes were classified as occurring or absent (not shown) for each 2 min-interval recorded. For ***all regimes*** together, occurrence of posture changes ranged from 9 % to 14 % (mean pre-visit: 12 %; tab. 5.3.1-39). <u>Immediately before the visit</u>, occurrence of posture changes was observed in 14 % of all sessions.

Concerning ***specific regimes***, posture changes prior to visitation were seen more often in FAs-C$_{1,2}$ (mean pre-visit: 19 %) than at the other regimes (pre-visit means FAs-B$_1$: 6 %, FAs-X: 13 %, and FAs-Y: 3 %). With respect to FAs-Y, the only occurrence of posture changes was observed in one session during the last pre-visit interval (2-1 min before the visit).

During human visitation (as compared to pre-visit behaviour), <u>increases</u> in occurrence of posture changes were observed far more frequently than decreases (tab. 5.3.1-40). <u>Increases</u> in occurrence

Table 5.3.1-39: Occurrence of Posture Changes <u>before</u> Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; Occur: occurring, n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Posture Changes (%)	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg **Occur**	12.12	13.95	8.51	9.80	13.73	11.62
FAs-B$_1$ **Occur**	*no %*	7.69	0.00	5.88	11.76	6.33
FAs-C$_{1,2}$ **Occur**	18.18	30.77	12.50	12.50	18.75	18.54
FAs-X **Occur**	16.67	9.09	16.67	16.67	8.33	13.48
FAs-Y **Occur**	0.00	0.00	0.00	0.00	16.67	3.33
n$_{(sess.)}$ FAs-allReg	33	43	47	51	51	n.a.
n$_{(sess.)}$ FAs-B$_1$	4	13	13	17	17	n.a.
n$_{(sess.)}$ FAs-C$_{1,2}$	11	13	16	16	16	n.a.
n$_{(sess.)}$ FAs-X	12	11	12	12	12	n.a.
n$_{(sess.)}$ FAs-Y	6	6	6	6	6	n.a.

of posture changes ranged from +5 % to +39 % (mean during-visit: +17 %) for ***all regimes*** together. Occurrence of posture changes increased markedly as the visitor(s) remained at 5 m distance from the focal nest (+39 %), followed by the values found for the visiting stages ‘visitor at 3 m’ (+27 %) and ‘visitor retreat’ (+23 %).

Specific regimes all had peak values during the visiting stage ‘visitor at 5 m’, but these were distinct only in FAs-B$_1$ and FAs-C$_{1,2}$ (not being the single highest value in the other two regimes). Moreover, visitor approaches to 5 m and to 3 m elicited a clear response in FAs-C$_{1,2}$ only (all other regimes: one session). With respect to FAs-X and FAs-Y, values for the visiting stage ‘retreat’ were as high as or higher than those during the visitors’ stay at 3 m, while in FAs-B$_1$ and FAs-C$_{1,2}$ values were lower.

The mean during-visit values were lowest for FAs-B$_1$ (+14 %), slightly higher FAs-C$_{1,2}$ and FAs-X (+17 % and +19 %, resp.), and highest for FAs-Y (+24 %).

Decreases in posture changes during human visitation were not observed in ***all regimes***; therefore no overall trend is described. As *for* ***specific regimes***, decreases in posture changes occurred in 2 sessions[35] only (one FA-B$_1$, one FA-C$_1$); both times, the focal animal had been engaged in regular posture changes (immediately) prior to visitation (appendix 5.3.1-1). A continuous decrease persisting throughout visitation was found in that specific FA-C$_1$ (starting when the visitor approached

Table 5.3.1-40: Occurrence and Prevalence of Posture Changes during Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, –: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded. **N.b.:** Except for two sessions from FAs-B$_1$ (% not shown), the visiting stages ‘visitor along colony (20-25 m)’ immediately pre-visit and post-visit applied only to FAs-C$_{1,2}$ and FAs-Y.

Posture Changes (%)	**visitor along colony (20-25m)**	**visitor approach to 15m**	**visitor @ 15m**	**visitor approach to 5m**	**visitor @ 5m**	**visitor approach to 3m**	**visitor @ 3m**	**visitor retreat**	**visitor along colony (20-25m)**	**mean during-visit**
FAs-allReg **+**	9.52	9.09	18.18	13.64	38.64	9.09	27.27	22.73	5.26	17.05
FAs-B$_1$ **+**	*no %*	14.29	7.14	7.14	42.86	0.00	28.57	14.29	n.a.	14.29
FAs-C$_{1,2}$ **+**	7.14	0.00	21.43	21.43	35.71	21.43	28.57	14.29	7.14	17.46
FAs-X **+**	n.a.	9.09	18.18	9.09	36.36	9.09	18.18	36.36	n.a.	19.48
FAs-Y **+**	20.00	20.00	40.00	20.00	40.00	0.00	40.00	40.00	0.00	24.44
FAs-allReg **–**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B$_1$ **–**	*no %*	0.00	0.00	0.00	-7.14	-7.14	-7.14	-7.14	n.a.	-3.57
FAs-C$_{1,2}$ **–**	0.00	-7.14	-7.14	-7.14	-7.14	-7.14	-7.14	-7.14	-7.14	-6.35
FAs-X **–**	n.a.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	n.a.	0.00
FAs-Y **–**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$n_{(sess.)}$ FAs-allReg	21	44	44	44	44	44	44	44	19	n.a.
$n_{(sess.)}$ FAs-B$_1$	2	14	14	14	14	14	14	14	0	n.a.
$n_{(sess.)}$ FAs-C$_{1,2}$	14	14	14	14	14	14	14	14	14	n.a.
$n_{(sess.)}$ FAs-X	0	11	11	11	11	11	11	11	0	n.a.
$n_{(sess.)}$ FAs-Y	5	5	5	5	5	5	5	5	5	n.a.

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[35] B4-2 and C1-1; recorded at different times of the morning of 24.11.2000.

to 15 m); in the above-mentioned session of FA-B$_1$, occurrence of posture changes decreased from the visitor's stay at 5 m until the end of visitation. Decreases in posture changes were never observed for FAs-X and FAs-Y.

After the visit (tab. 5.3.41), increases in occurrence of posture changes (as compared to pre-visit) were observed far more frequently than decreases.

Increases in occurrence of posture changes ranged from +12 % (9-10 min post-visit) to +28 % (5-6 min post-visit) for ***all regimes*** together. Values for increased occurrence of posture changes rose during the first 3 post-visit intervals, with the maximum value calculated for the third. Subsequently they waned, and the lowest value was obtained for the fifth post-visit interval.

The mean post-visit value for increased occurrence of posture changes (+19 %) was slightly higher than the respective during-visit value (+17 %).

Specific regimes exhibited differences with respect to location of peak value: Values for FAs-Y peaked in the second post-visit interval, for FAs-B$_1$ and FAs-C$_{1,2}$ in the third post-visit interval, and for FAs-X in the fourth post-visit interval. The peak value was most pronounced for FAs-B$_1$.

The mean post-visit values were similar[36] for FAs-B$_1$ and FAs-Y (+25 %) and similar for FAs-C$_{1,2}$ and FAs-X (+15 % and +16 %, resp.). Comparison to mean during-visit values showed pronounced differences for FAs-B$_1$ only (mean during-visit: +14 % vs. mean post-visit: +25 %).

Decreases in occurrence of posture changes were only observed in one bird of FAs-B$_1$ (same bird as during visitation); therefore, no overall trend is described. This focal animal had been engaged in regular posture changes (immediately) prior to visitation (appendix 5.3.1-1).

Table 5.3.1-41: Occurrence and Prevalence of Posture Changes after Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **+**: increase as compared to pre-visit, –: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded.

Posture Changes (%)	1-2min post-visit	3-4min post-visit	5-6min post-visit	7-8min post-visit	9-10min post-visit	mean post-visit
FAs-allReg **+**	15.91	22.73	27.91	18.60	12.20	19.47
FAs-B$_1$ **+**	21.43	28.57	42.86	14.29	15.38	24.51
FAs-C$_{1,2}$ **+**	14.29	14.29	23.08	15.38	7.69	14.95
FAs-X **+**	9.09	18.18	18.18	27.27	9.09	16.36
FAs-Y **+**	20.00	40.00	20.00	20.00	*no %*	25.00
FAs-allReg **–**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B$_1$ **–**	0.00	0.00	-7.14	-7.14	-7.69	-4.40
FAs-C$_{1,2}$ **–**	0.00	0.00	0.00	0.00	0.00	0.00
FAs-X **–**	0.00	0.00	0.00	0.00	0.00	0.00
FAs-Y **–**	0.00	0.00	0.00	0.00	*no %*	0.00
$n_{(sess.)}$ FAs-allReg	44	44	43	43	41	n.a.
$n_{(sess.)}$ FAs-B$_1$	14	14	14	14	13	n.a.
$n_{(sess.)}$ FAs-C$_{1,2}$	14	14	13	13	13	n.a.
$n_{(sess.)}$ FAs-X	11	11	11	11	11	n.a.
$n_{(sess.)}$ FAs-Y	5	5	5	5	4	n.a.

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36 same, once rounded off

An increased occurrence of posture changes was never observed in response to **conspecific** ‘stationary’ presence at the focal nest, or conspecific movement at the focal nest. In only 1 of 44 sessions, increased conspecific movement (irrespective of distance from the focal nest) appeared to elicit an increased occurrence of posture changes.

Skua low overflights coincided with increased posture changes in 1 of 14 sessions, while neither skua presence on the ground (6 sessions) nor **aircraft** noise (3 sessions) were ever associated with an increased occurrence of posture changes.

For these disturbance types, a decrease in occurrence of posture changes was never observed (appendix 5.3.1-1).

5.3.1.11 Heart Rate Changes

N.b.: Unlike behaviour systems or posture changes, heart rate could not be categorised as ‘predominant’ ‘occurring’, or ‘absent’; instead, differences between periods were appraised by assessing deviations from a suavely undulating ‘baseline’ heart rate. In order to gauge increases/ decreases during- and post-visit, it was necessary to first examine these deviations pre-visit.

Only sessions during which heart rate had been obtained were used for visual appraisal. For each session, stable pre-visitation heart rate (the ‘regularly undulating wave-line’) was considered the current baseline.

Recapitulation: Heart rate is defined to ‘undulate regularly’ if values from successive 20 s-counts differ by one or two beats without, however, resulting in a trend (increase/ decrease). These ‘undulations’ are considered ‘physiologically normal’.

Summing up, heart rate prior to visitation was most frequently appraised as ‘undulating regularly’ (FAs-allReg mean pre-visit: 82 %). While mean during-visit values for regularly undulating heart rate still amounted to 62 % (FAs-allReg), increases (as compared to pre-visit) constituted the main change observed in heart rate both during (max. during-visit value FAs-allReg: +80 %) and after visitation (max. post-visit value: +25 %).

Comparing disturbance types (human visitation, conspecific disturbance, skua/ aircraft disturbance; FAs-allReg), increased heart rate was found both during and after **human** visitation, with mean during-visit values (+37 %) approximately twice as high as mean post-visit ones (+19 %).

Increased heart rate did not constitute a consistent reaction towards **conspecifics** (appendix 5.3.1-1). It was observed in 1 of 3 sessions where a **skua** had been present on the ground, but not in response to skua low overflights (0 of 8 sessions) or **aircraft** disturbance (0 of 1 session). Decreased heart rate in response to these disturbance types was never observed.

Comparing visiting stages and post-visit 2 min-intervals (FAs-allReg), the **highest mean-values** for increased heart rate (+80 % and +62 %, resp.) were found during visitor approach to 5 m and to 3 m during visitation, followed by values obtained during visitor stay at the respective distances from the focal-animal nest (at 5 m: +45 %, at 3 m: +42 %) and during visitor retreat (+41 %). Post-visitation values were considerably lower, with maximum values calculated for the first (1-2 min; +25 %) and fourth (7-8 min; +20 %) post-visit intervals.

Antidirectional changes during visitation were predominantly observed between increased heart rate and decreased resting behaviour, with peak numbers during approaches to 5 m and 3 m, and only slightly lower numbers for visitor stay at these distances.

After visitation, they were almost exclusively observed between increased heart rate and decreased resting behaviour, with the peak value located in the first post-visit interval (1-2 min).

Syndirectional changes were (almost) exclusively found for increased heart rate, both during and after visitation (one exception during-visit): In combination with increased vigilance behaviour, they occurred throughout the visit, with peak numbers calculated for the approach to 5 m, stay at 5 m and the approach to 3 m during visitation. At 5 m distance from the focal nest, conjunctions with increased scattering, breeding, occurrence of headshakes and posture changes were also frequently observed. Increased agonistic behaviour mainly coincided with increased heart rate during visitor approach to 3 m, while increased scattering alongside increased heart rate was additionally prominent during visitor stay at 3 m.

Across all post-visit intervals, increased heart rate most often occurred together with increased vigilance, and also in conjunction with scattered behaviour, breeding behaviour, occurrence of headshakes, and posture changes. It was never associated with comfort behaviour and only rarely with agonistic or resting behaviour. Peak values for increased heart rate coinciding with increased vigilance, with increased occurrence of headshakes, and with increased scattering, were calculated during the first post-visit interval (1-2 min); the other combinations did not exhibit peaks.

Comparing FAs subjected to different regimes, from visitor approach to 5 m onwards up until and including visitor retreat FAs-B_1 (mean during-visit: +48 %) and FAs-Y (no mean value calculated, but all available FAs responding) exhibited more persistent increases in heart rate than FAs-X (mean during-visit: +43 %) and particularly FAs-$C_{1,2}$ (mean during-visit: +28 %). The **highest value** was obtained from FAs-B_1 during the visiting stage ‘visitor approach to 5 m’ (+88 %).

During visitation, FAs subjected to different visiting regimes showed only slight temporal differences with respect to **peak values**: In all regimes, maximum values were calculated for the visiting stage ‘visitor approach to 5 m’, but these constituted ‘true peak values’ only for FAs-B_1 and FAs-X. For FAs-$C_{1,2}$, the same maximum value (+67 %) was again obtained during visitor approach to 3 m (twin peaks), while – as stated above – all available FAs-Y responded in visiting stages following and including visitor approach to 5 m.

Increased heart rate throughout the post-visit period was found for FAs-B_1 in a fluctuating number of sessions. As for FAs-$C_{1,2}$, increased heart rate after visitation persisted until and including the fourth post-visit interval (7-8min). For FAs-X, increases in heart rate were found only in the third and fifth post-visit intervals, and for FAs-Y in the first, fourth and fifth post-visit intervals.

“Curiouser and Curiouser”: Heart rate increases without any overt behavioural changes were mainly noted during the visiting stages of approach (4 times to 15 m, and 4 times to 5 m), and once for two consecutive stages (at 5 m and approach to 3 m). In contrast, only one ‘unaccompanied increase’ occurred after visitation (last post-visit interval).

General findings: Due to intermittent illegibility of heart rate (e.g., prone penguins getting up), numbers of heart rate records differed between intervals in all periods. **Pre-**visit, heart rate records were available for 18 (10-8 min pre-visit) to 30 sessions (4th and 5th pre-visit intervals, 4-1 min pre-visit), for 22 (retreat) to 29 sessions (visitor at 5 m) **during**-visit[36] , and for 24 (1-2 min post-visit) to 30 sessions (7-8 min post-visit) **post**-visit.

Prior to human visitation, heart rate was categorised as 'undulating regularly', increasing, or decreasing for each pre-visit interval. Regularly undulating heart rate was most common for the majority of pre-visit periods in ***all regimes*** (FAs-allReg, range: 78 % to 87 %; mean pre-visit: 82 %; tab. 5.3.1-42. Increases occurred slightly more often than decreases. Frequently, increases in one interval were complemented by decreases of similar amplitude in the same[37] or the following interval (appendix 5.3.1-1; appendix 5.3.1-2.10).

Immediately before the visit (2-1 min pre-visit), regularly undulating heart rate was recorded in 80 % of the sessions.

Concerning ***specific regimes***, undulating heart rate was the 'default' pattern for all of them. It was 'least' frequently observed at FAs C$_{1,2}$ (mean pre-visit: 73 %), more often at FAs-B$_1$ (81 %) and FAs-X (84 %), and always at FAs-Y (all pre-visit intervals in 4 of 4 sessions).

Table 5.3.1-42: Heart Rate before Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **~**: undulating regularly; **+**: increase as compared to 'undulating baseline', **–**: decrease as compared to 'undulating baseline'; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded; *never*: never observed; 0 of 4: with respect to FAs-Y, all values were based on less than 5 sessions and therefore made explicit; grey-scale stripes follows same code as coloured cells.

Heart Rate (%)	**10-9min pre-visit**	**8-7min pre-visit**	**6-5min pre-visit**	**4-3min pre-visit**	**2-1min pre-visit**	**mean pre-visit**
FAs-allReg ~	77.78	79.17	85.71	86.67	80.00	81.87
FAs-B$_1$ ~	*no %*	100.00	88.89	72.73	63.64	81.31
FAs-C$_{1,2}$ ~	66.67	57.14	70.00	90.00	80.00	72.76
FAs-X ~	60.00	60.00	100.00	100.00	100.00	84.00
FAs-Y ~	4 of 4	4 of 4	4 of 4	4 of 4	4 of 4	4 of 4
FAs-allReg **+**	16.67	8.33	10.71	13.33	16.67	13.14
FAs-B$_1$ **+**	*no %*	0.00	11.11	27.27	36.36	18.69
FAs-C$_{1,2}$ **+**	33.33	14.29	20.00	10.00	10.00	17.52
FAs-X **+**	20.00	20.00	0.00	0.00	0.00	8.00
FAs-Y **+**	0 of 4	0 of 4	0 of 4	0 of 4	0 of 4	*never*
FAs-allReg **–**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B$_1$ **–**	*no %*	0.00	0.00	0.00	0.00	*never*
FAs-C$_{1,2}$ **–**	0.00	-28.57	-10.00	0.00	-10.00	-9.71
FAs-X **–**	-20.00	-20.00	0.00	0.00	0.00	-8.00
FAs-Y **–**	0 of 4	0 of 4	0 of 4	0 of 4	0 of 4	*never*
n$_{(sess.)}$ FAs-allReg	18	24	28	30	30	n.a.
n$_{(sess.)}$ FAs-B$_1$	3	8	9	11	11	n.a.
n$_{(sess.)}$ FAs-C$_{1,2}$	6	7	10	10	10	n.a.
n$_{(sess.)}$ FAs-X	5	5	5	5	5	n.a.
n$_{(sess.)}$ FAs-Y	4	4	4	4	4	n.a.

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[36] For the visiting stages that only applied to FAs-C$_{1,2}$ and FAs-Y, records were available for 15 (visitor along colony – pre-visit) and 8 sessions (visitor along colony – post-visit), respectively.

[37] In these cases, the initial change was used to characterise the interval, i.e., increase-decrease → increase; whereas decrease-increase → decrease.

For FAs-B_1, increases in heart rate spanning more than one interval were measured in three sessions[38]: In one session, the increase lasted 3 intervals, in a further two sessions increases were observed for 2 consecutive intervals (appendix 5.3.1-2.10). With respect to FAs-Y, an increase in heart rate was not observed for any of the pre-visit intervals.

Prior to visitation, a decrease in heart rate was not observed at ***all regimes***; therefore, no overall trend is provided. Decreases in heart rate (below the regularly undulating wave-line) were found for FAs-$C_{1,2}$ (for 1 interval each in 4 sessions of 3 different FAs)[39] and FAs-X (for 1 interval each in 2 sessions of 2 different FAs)[40]. They were not observed for FAs-B_1 and FAs-Y (appendix 5.3.1-1).

During human visitation, proportions for regularly undulating heart rate dropped markedly (as compared to pre-visit heart rate), and increases in heart rate occurred far more frequently than decreases (tab. 5.3.1-43).

Looking at ***all regimes*** together, increases in heart rate ranged from 0 % to +80 % (mean during-visit FAs-allReg: +37 %). Marked increases became apparent as early as during visitor approach to 15 m (+37 %), and remained prominent up until and including the stage of visitor retreat (+41 %). The highest values were found during visitor approach to 5 m (+80 %), and to 3 m (+62 %). For some focal birds, heart rate also remained elevated during visitor stay at a fixed distance (visitor at 15 m/ 5 m/ 3 m; see appendix 5.3.1-1). Visitor stay at 15 m, in contrast, elicited heart rate increases in only 24 % of all sessions.

As for ***specific regimes***, for FAs-$C_{1,2}$, proportions for increased heart rate were often less prominent than at the other regimes (range: +10 % to +67 %), particularly during visitor stay at 3 m and visitor retreat (+14 % each). Concerning FAs-Y, birds showed increased heart rate during the visitors' approach to 15 m in 3 of 4 sessions; in 1 of 2 sessions they did so during the visitors' stay at 15 m; and in all sessions 'available' birds exhibited increased heart rate from approach to 5 m up until and including visitor retreat ('peak plateau'). With respect to FAs-B_1 and FAs-X, visitor approach to 5 m elicited the most pronounced increase (+88 % and +83 %, resp.), while values obtained during visitor approach to 3 m' were lower (+60 % and +40 %, resp.). Peak values for FAs-$C_{1,2}$ (+67 %) occurred at visitor approach to 5 m as well as to 3 m.

The mean during-visit value was substantially lower for FAs-$C_{1,2}$ (+28 %) than for FAs-B_1 and FAs-X (+48 % and +43 %, resp.). With respect to FAs-Y, no mean is presented (due to low number of sessions), but 'spelt-out' table-entries show that maximally (all sessions available) increased heart rate persisted from visitor approach to 5 m until retreat.

A decrease in heart rate during human visitation was observed only once[41] (1 FA-X, visiting stage: visitors at 3 m), and never encountered in the other FAs.

In 3 sessions (appendix 5.3.1-1), heart rate throughout the visit did not change as compared to pre-visit heart rate. For these, pre-visit heart rate had exhibited different patterns (once[42] 'undulating regularly' within the only 2 min-interval for which pre-visit heart rate had been recorded; twice[43] 'increasing in all intervals').

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[38] B3-1, on 13 Nov. 2000 (afternoon); B3-1, B4-2, on 24 Nov. 2000 (morning)

[39] C1-1, on 20 Nov. 2000 (morning); C2-2, on 17 Nov. (afternoon) and 26 Nov. 2000 (afternoon); C11-1, on 26 Nov. (do.)

[40] X1-1, on 26 Nov 2001 (morning); X2-1, on 23 Nov. 2001 (afternoon)

[41] X1-1, on 26 Nov. 2001 (morning)

[42] C2-2, on 21 Nov. 2000 (afternoon)

[43] B3-1, on 13 Nov. 2000 (afternoon), and 24 Nov. 2000 (morning)

Table 5.3.1-43: Occurrence and Prevalence of Heart Rate Changes during Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; **~**: undulating regularly; **+**: increase as compared to pre-visit, –: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded; *once*: observed only once; *never*: never observed; 0 of 4: with respect to FAs-Y, all values were based on less than 5 sessions and therefore made explicit; grey-scale follows same code as coloured cells. **N.b.:** Except for two sessions from FAs-B$_1$ (% not shown), the visiting stages 'visitor along colony (20-25 m)' immediately pre-visit and post-visit applied only to FAs-C$_{1,2}$ and FAs-Y.

Heart Rate (%)	**visitor along colony (20-25m)**	**visitor approach to 15m**	**visitor @ 15m**	**visitor approach to 5m**	**visitor @ 5m**	**visitor approach to 3m**	**visitor @ 3m**	**visitor retreat**	**visitor along colony (20-25m)**	**mean during-visit**
FAs-allReg **~**	93.33	62.96	76.00	20.00	55.17	38.46	54.17	59.09	100.00	62.13
FAs-B$_1$ **~**	*no %*	66.67	77.78	12.50	60.00	40.00	50.00	60.00	n.a.	52.42
FAs-C$_{1,2}$ **~**	90.00	77.78	77.78	33.33	60.00	33.33	85.71	85.71	100.00	71.52
FAs-X **~**	n.a.	60.00	80.00	16.67	66.67	60.00	40.00	*no %*	n.a.	53.89
FAs-Y **~**	4 of 4	1 of 4	1 of 4	0 of 4	0 of 4	0 of 4	0 of 4	0 of 4	1 of 4	*no %*
FAs-allReg **+**	6.67	37.04	24.00	80.00	44.83	61.54	41.67	40.91	0.00	37.41
FAs-B$_1$ **+**	*no %*	33.33	22.22	87.50	40.00	60.00	50.00	40.00	n.a.	47.58
FAs-C$_{1,2}$ **+**	10.00	22.22	22.22	66.67	40.00	66.67	14.29	14.29	0.00	28.48
FAs-X **+**	n.a.	40.00	20.00	83.33	33.33	40.00	40.00	*no %*	n.a.	42.78
FAs-Y **+**	0 of 4	3 of 4	1 of 2	2 of 2	3 of 3	2 of 2	2 of 2	1 of 1	0 of 1	*no %*
FAs-allReg **–**	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
FAs-B$_1$ **–**	*no %*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	n.a.	*never*
FAs-C$_{1,2}$ **–**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	*never*
FAs-X **–**	n.a.	0.00	0.00	0.00	0.00	0.00	-20.00	*no %*	n.a.	*once*
FAs-Y **--**	0 of 4	0 of 4	0 of 4	0 of 4	0 of 4	0 of 4	0 of 4	0 of 4	0 of 4	*never*
n$_{(sess.)}$ FAs-allReg	15	27	25	25	29	26	24	22	8	n.a.
n$_{(sess.)}$ FAs-B$_1$	1	9	9	8	10	10	10	10	0	n.a.
n$_{(sess.)}$ FAs-C$_{1,2}$	10	9	9	9	10	9	7	7	7	n.a.
n$_{(sess.)}$ FAs-X	0	5	5	6	6	5	5	4	0	n.a.
n$_{(sess.)}$ FAs-Y	4	4	2	2	3	2	2	1	1	n.a.

Following, changes in heart rate were examined in relation to changes in behaviour systems. For this, antidirectional changes (increased heart rate coinciding with decreases in behaviour systems and vice versa[44]) as well as syndirectional changes (increases in heart rate accompanied by increases in behavioural systems/ decreases accompanied by other decreases) were investigated during each visiting stage. Table 5.3.1-44 gives an overview of during-visit antidirectional changes.

The vast majority of such combinations were observed between increased heart rate and decreased resting behaviour. Except for the visiting stage 'visitor along colony – post-visit', the combination was found throughout the visit, with peak numbers (13 and 12, resp.) during approaches to 5 m and 3 m. For visitor stay at these distances, numbers were only slightly lower (11 and 10, resp.).

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[44] N.b.: This table does not provide information on occurrences of heart rate increase/ decrease unaccompanied by decreases/ increases in behaviour systems.

Table 5.3.1-44: <u>During-Visit</u> Changes in Heart Rate in Conjunction with Antidirectional Changes in Behaviour Systems and Posture. For each visiting stage, entries represent numbers of sessions in which a particular conjunction was observed (FAs-allReg). Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_{1}$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_{1}$: 1 P, L&F; FAs-C$_{1}$: 1 P, S&S; FAs-C$_{2}$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; HR: Heart Rate, Sctt: Scattered Behaviour, R: Resting, C: Comfort, B: Breed, V: Vigilance, A: Agonistic Behaviour; H: Headshakes, P: Posture Changes; HR**+**: increase, HR–: decrease. **N.b.:** Except for two sessions from FAs-B$_{1}$, the visiting stages 'along colony – pre' and 'along colony – post' applied only to FAs-C$_{1,2}$ and FAs-Y.

Decreases in Heart Rate Coinciding with Increases in Behaviour Systems and Posture										**Increases** in Heart Rate Coinciding with Decreases in Behaviour Systems and Posture									
HR– coincides with	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post	**HR+** coincides with	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post
Sctt+	o	o	o	o	o	o	o	o	o	**Sctt–**	o	1	o	1	1	1	2	o	o
R+	o	o	o	o	o	o	o	o	o	**R–**	1	5	6	13	11	12	10	8	o
C+	o	o	o	o	o	o	o	o	o	**C–**	o	1	o	1	1	2	1	o	o
B+	o	o	o	o	o	o	o	o	o	**B–**	o	1	o	1	o	o	1	o	o
V+	o	o	o	o	o	o	1	o	o	**V–**	o	o	o	1	o	o	1	o	o
A+	o	o	o	o	o	o	o	o	o	**A–**	o	o	o	o	o	o	o	o	o
H+	o	o	o	o	o	o	o	o	o	**H–**	o	o	o	o	o	o	o	o	o
P+	o	o	o	o	o	o	o	o	o	**P–**	o	o	o	o	o	2	1	o	o

<u>Decreased</u> heart rate was observed only once[45] , and on this occasion occurred in conjunction with increased vigilance (appendix 5.3.1-2.10).

In addition, table 5.3.1-45 provides information on <u>syndirectional changes</u>. Throughout the visit, <u>increased</u> heart rate most often occurred together with increased vigilance behaviour, with peak numbers (11) during the approach to 5 m, stay at 5 m, and the approach to 3 m.

Additionally, during the visiting stage 'visitor at 5 m', it coincided with increased breeding behaviour, occurrence of headshakes, and posture changes. Scattered behaviour increased syndirectionally with heart rate mainly during visitor stay at 5 m and at 3 m, respectively, while increased agonistic behaviour in conjunction with increased heart rate was most prominent during the visiting stage 'visitor approach to 3 m'.

During the only recording of <u>decreased</u> heart rate[46] , resting behaviour decreased simultaneously (appendix 5.3.1-2.10).

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[45] X1-1, on 26 Nov. 2001 (morning) during the visiting stage 'visitors at 3 m'

[46] as mentioned for antidirectional changes, X1-1, on 26 Nov. 2001 (morning), visiting stage 'visitors at 3 m'

Table 5.3.1-45: <u>During-Visit</u> Changes in Heart Rate in Conjunction with Syndirectional Changes in Behaviour Systems and Posture. For each visiting stage, entries represent numbers of sessions in which a particular conjunction was observed (FAs-allReg). Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; HR: Heart Rate, Sctt: Scattered Behaviour, R: Resting, C: Comfort, B: Breed, V: Vigilance, A: Agonistic Behaviour; H: Headshakes, P: Posture Changes; HR**+**: increase, HR–: decrease. **N.b.:** Except for two sessions from FAs-B$_1$, the visiting stages 'along colony – pre' and 'along colony – post' applied only to FAs-C$_{1,2}$ and FAs-Y.

Decreases in Heart Rate Coinciding with Decreases in Behaviour Systems and Posture										**Increases** in Heart Rate Coinciding with Increases in Behaviour Systems and Posture									
HR– coincides with	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post	**HR+** coincides with	along colony - pre	approach to 15m	@ 15m	approach to 5m	@ 5m	approach to 3m	@ 3m	retreat	along colony - post
Sctt–	o	o	o	o	o	o	o	o	o	**Sctt+**	o	o	4	4	7	4	5	3	o
R–	o	o	o	o	o	o	1	o	o	**R+**	o	o	o	1	o	o	o	o	o
C–	o	o	o	o	o	o	o	o	o	**C+**	o	o	o	o	o	o	o	o	o
B–	o	o	o	o	o	o	o	o	o	**B+**	o	o	1	1	6	1	3	1	o
V–	o	o	o	o	o	o	o	o	o	**V+**	1	5	5	11	11	11	9	8	o
A–	o	o	o	o	o	o	o	o	o	**A+**	o	o	3	2	1	6	3	1	o
H–	o	o	o	o	o	o	o	o	o	**H+**	o	o	2	2	7	3	4	1	o
P–	o	o	o	o	o	o	o	o	o	**P+**	o	o	1	1	6	1	2	o	o

Increased heart rate also occurred without overt behavioural changes. Within these datasets, '<u>unaccompanied increases</u>' were noted for 1 visiting stage each in 8 different sessions, and for 2 consecutive stages in a further session. They occurred 4 times during visitor approach to 15 m, 4 times during visitor approach to 5 m, and once during the visiting stages 'visitor at 5 m' and 'visitor approach to 3 m' (appendix 5.3.1-2.10).

After the visit (tab. 5.3.1-46), occurrences of <u>increased</u> heart rate (as compared to pre-visit) persisted throughout the post-visit period, while decreased heart rate was never observed.

Mean values for regularly undulating heart rate calculated for ***all regimes*** together were very close to the pre-visit mean (mean pre-visit FAs-allReg: 82 %; tab. 5.3.1-42; mean post-visit FAs-allReg: +81 %). Comparing post-visit intervals to the respective pre-visit intervals equally far away from human visitation (i.e., first pre-visit to fifth post-visit, second pre-visit to fourth post-visit), post-visit values for undulating heart rate were slightly lower during the first three intervals (1-6 min post-visit vs. 6-1min pre-visit) and slightly higher during the remaining two intervals (7-10 min post-visit vs. 10-7 min pre-visit).

Values for <u>increased</u> heart rate for ***all regimes*** together were highest in the first post-visit interval (+25 %), and continued to fluctuate between +15 % and +20 % in the following intervals (mean post-visit: +19 %).

Table 5.3.1-46: Occurrence and Prevalence of Heart Rate Changes after Human Visitation. For comparison, proportional values are shown. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; ~: undulating regularly; **+**: increase as compared to pre-visit, –: decrease as compared to pre-visit; n (sess.): number of sessions proportion is based on; n.a.: not applicable; *no %*: value based on less than 5 sessions and thus excluded; *never*: never observed; 0 of 4: with respect to FAs-Y, all values were based on less than 5 sessions and therefore made explicit; grey-scale follows same code as coloured cells.

Heart Rate (%)	**1-2min post-visit**	**3-4min post-visit**	**5-6min post-visit**	**7-8min post-visit**	**9-10min post-visit**	**mean post-visit**
FAs-allReg ~	75.00	84.62	84.62	80.00	82.14	81.27
FAs-B_1 ~	66.67	77.78	88.89	72.73	90.00	79.21
FAs-$C_{1,2}$ ~	77.78	80.00	80.00	80.00	100.00	83.56
FAs-X ~	*no %*	100.00	80.00	100.00	60.00	85.00
FAs-Y ~	1 of 2	2 of 2	2 of 2	3 of 4	2 of 4	*no %*
FAs-allReg **+**	25.00	15.38	15.38	20.00	17.86	18.73
FAs-B_1 **+**	33.33	22.22	11.11	27.27	10.00	20.79
FAs-$C_{1,2}$ **+**	22.22	20.00	20.00	20.00	0.00	16.44
FAs-X **+**	*no %*	0.00	20.00	0.00	40.00	15.00
FAs-Y **+**	1 of 2	0 of 2	0 of 2	1 of 4	2 of 4	*no %*
FAs-allReg **–**	0.00	0.00	0.00	0.00	0.00	*never*
FAs-B_1 **–**	0.00	0.00	0.00	0.00	0.00	*never*
FAs-$C_{1,2}$ **–**	0.00	0.00	0.00	0.00	0.00	*never*
FAs-X **–**	*no %*	0.00	0.00	0.00	0.00	*never*
FAs-Y **–**	0 of 2	0 of 2	0 of 2	0 of 4	0 of 4	*never*
$n_{(sess.)}$ FAs-allReg	24	26	26	30	28	n.a.
$n_{(sess.)}$ FAs-B_1	9	9	9	11	10	n.a.
$n_{(sess.)}$ FAs-$C_{1,2}$	9	10	10	10	9	n.a.
$n_{(sess.)}$ FAs-X	4	5	5	5	5	n.a.
$n_{(sess.)}$ FAs-Y	2	2	2	4	4	n.a.

The mean post-visit value for increased heart rate (+19 %) was still half the mean during visit-value (+37 %), suggesting that for some birds, a good measure of responsiveness persisted during the post-visit period.

With respect to ***specific regimes***, only for FAs-B_1 increased heart rate was found during each post-visit interval (1-10 min) in at least one session. As regards FAs-$C_{1,2}$, focal animals exhibited increased heart rate until the fourth (1-8 min), but not in the fifth post-visit interval. With respect to FAs-X, increased heart rate was found in the third (5-6 min) and fifth (9-10 min) post-visit interval, while for FAs-Y, increased heart rate was observed during the first (1-2 min), fourth (7-8 min) and fifth (9-10 min) post-visit intervals.

Mean post-visit values remained highest for FAs-B_1 (+21 %), and were lower and roughly equal for FAs-$C_{1,2}$ and FAs-X (+16 % and +15 %, resp.). Due to low number of sessions, no mean value is presented for FAs-Y.

As regards FAs-B_1 (+21 %) and FAs-X (+15 %), mean post-visit values were approximately 0.4 times mean during-visit values (tab. 5.3.1-43). Owing to the comparatively low mean during-visit value, the difference was least pronounced for FAs-$C_{1,2}$ (+17 %), with the mean post-visit value being approx. 0.6 times the mean during-visit one.

A decrease in heart rate (below the regularly undulating wave-line) was never observed during the post-visit period.

No change in heart rate as compared to pre-visit was found in 13 sessions, comprising very different pre-visit heart rate patterns (from ‘undulating regularly throughout’ to ‘increasing in most intervals’; appendix 5.3.1-2.10).

Following, changes in heart rate were examined in relation to changes in behaviour systems. Table 5.3.1-47 gives an overview of post-visit antidirectional changes.

Combinations were almost exclusively observed between increased heart rate and decreased resting behaviour (summed up across all post-visit intervals: 15 times). They were most pronounced in the two minutes following cessation of visit (first post-visit interval: 6 sessions), but occurred in all post-visit intervals (3-4 min and 7-8 min: 3 sessions; 9-10 min: 2 sessions; 5-6 min: 1 session).

Table 5.3.1-47: Post-Visit Changes in Heart Rate in Conjunction with Antidirectional Changes in Behaviour Systems. For each 2 min-interval, entries represent numbers of sessions in which a particular conjunction was observed (FAs-allReg). Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; min 1-2:1st Post-visit Interval, comprising the first 2 min after the visit had ended; HR: Heart Rate, Sctt: Scattered Behaviour, R: Resting, B: Breed, C: Comfort, V: Vigilance, A: Agonistic Behaviour; H: Headshakes, P: Posture Changes; HR**+**: increase, HR–: decrease. n.a.: no decreases in heart rate observed, hence no combinations possible.

Decreases in Heart Rate Coinciding with Increases in Behaviour Systems and Posture						**Increases** in Heart Rate Coinciding with Decreases in Behaviour Systems and Posture					
HR– coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10	**HR+** coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10
Sctt+	n.a.					**Sctt–**	o	o	o	o	1
R+						**R–**	**6**	3	1	3	2
C+						**C–**	o	o	o	o	o
B+						**B–**	o	o	o	o	o
V+						**V–**	o	o	o	o	1
A+						**A–**	o	o	o	o	o
H+						**H–**	o	o	o	o	o
P+						**P–**	o	o	o	o	o

In addition, table 5.3.1-48 provides information on syndirectional changes. Across all post-visit intervals, increased heart rate most often occurred together with increased vigilance (11 times), scattered behaviour (9 times), breeding behaviour (9 times), occurrence of headshakes (8 times) and posture changes (8 times). It was never associated with comfort behaviour and only rarely with agonistic (twice) or resting behaviour (once).

As for temporal patterns, increased heart rate alongside breeding behaviour as well as alongside posture changes was exhibited in 2 sessions in most post-visit intervals, whereas the combinations of heart rate and vigilance, occurrence of headshakes, and also heart rate and scattered behaviour, yielded more responses during the first than during the following post-visit intervals.

Within these datasets, an ‘unaccompanied increase’ (increased heart rate without overt behavioural changes in either direction) was found only once[47] (in the last post-visit interval; appendix 5.3.1-2.10).

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[1] B3-2, on 14 Nov. 2000 (morning)

Table 5.3.1-48: Post-Visit Changes in Heart Rate in Conjunction with Syndirectional Changes in Behaviour Systems. For each 2 min-interval, entries represent numbers of sessions in which a particular conjunction was observed (FAs-allReg). Entries comprising 5 sessions and more have been rendered prominent; o: empty category. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; min 1-2: 1st Post-visit Interval, comprising the first 2 min after the visit had ended; HR: Heart Rate, Sctt: Scattered Behaviour, R: Resting, B: Breed, C: Comfort, V: Vigilance, A: Agonistic Behaviour; H: Headshakes, P: Posture Changes; HR**+**: increase, HR–: decrease. n.a.: no decreases in heart rate observed, hence no combinations possible.

Decreases in Heart Rate Coinciding with Decreases in Behaviour Systems and Posture						**Increases** in Heart Rate Coinciding with Increases in Behaviour Systems and Posture					
HR– coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10	**HR+** coincides with	min 1-2	min 3-4	min 5-6	min 7-8	min 9-10
Sctt–	n.a.					**Sctt+**	3	2	1	2	1
R–						**R+**	o	o	o	o	1
C–						**C+**	o	o	o	o	o
B–						**B+**	2	2	1	2	2
V–						**V+**	5	1	1	2	2
A–						**A+**	1	o	1	o	o
H–						**H+**	3	2	1	1	1
P–						**P+**	2	2	1	2	1

Increases in heart rate were not found as a response to **conspecific** ‘stationary’ presence at the focal nest or to conspecific movement at the focal nest (appendix 5.3.1-1). As for FAs-B$_1$, increased conspecific movement (irrespective of distance from the focal nest) coincided with increases in heart rate in 3 of 11 sessions from 2 different focal animals[48]. On one occasion[49] (of a total of 3 sessions), **skua** presence on the ground and close to the focal nest elicited an increase in heart rate. Heart rate increases were found neither during skua low overflights (8 sessions) nor during **aircraft noise** (1 session only).

For these disturbance types, decreases in heart rate were never observed.

5.3.1.12 Regime Differences as Detected by Visual Appraisal

Recapitulation: In terms of severity, loud and fast visitation (L&F) is hypothesised to exceed impact of silent and slow visitation (S&S), while 3 visitors (3 P) are assumed to exert a greater impact than 1 visitor (1 P). Ranking the regimes employed in this study, the following order would ensue:

3 P, L&F (FAs-Y) > 1 P, L&F (FAs-B$_1$; FAs-C$_2$) $\geq$ 3 P, S&S (FAs-X) > 1 P, S&S (FAs-C$_1$)

N.b.: In the text, FAs-C$_{1,2}$ will henceforth be summarily referred to as having been subjected to ‘predominantly the regime 1 P, S&S’, as next to no difference in comportment had been observed in the first session following the switch in regimes (to 1 P, L&F).

Summing up, regime differences were examined with respect to the proportion of birds responding to human visitation during a given visiting stage/ post-visit interval. Visual appraisal emphasised the utility of looking at several comportment parameters conjointly as well as at ‘isolated’ parameters.

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[48] B3-1, on 24 Nov. 2000 (morning) and on 26 Nov. 2000 (afternoon); B3-2, on 14 Nov. 2000 (morning)

[49] B3-2, on 14 Nov. 2000 (morning)

Graded responses tallying with hypothesised severity of regime and/ or differential severity of visitor conduct (loud and fast vs. silent and slow) were found for each visiting stage (with the exception of the very shortest, viz., ‘visitor approach to 3m’) and each post-visit interval. The comportment parameters for which these graded responses were observed, however, differed between stages/ intervals. Graded responses were observed for all[50] comportment parameters save agonistic behaviours.

Adding up rank positions encountered at each visiting stage and each post-visit interval revealed an overall greater number of most pronounced responses for FAs-Y (3 P, L&F), complemented by an overall greater number of least pronounced responses for FAs-$C_{1,2}$ (predominantly 1 P, S&S), with intermediate positions for the remaining two regimes.

Separate examination of visit and post-visit periods supported hypothesised severity of regime with respect to rank positions most frequently occupied **during** visitation: FAs-Y were most often encountered on ranks ±4 (most pronounced response), FAs-B_1 (1 P, L&F) on ranks ±3, FAs-X (3 P, S&S) on ranks ±2, and FAs-$C_{1,2}$, on ranks ±1 (least pronounced response).

After visitation, rank ±4 was most frequently occupied by FAs-B_1 and slightly less frequently by FAs-Y (conduct-mediated). Highest number of ranked responses for third ranks (±3) was observed at FAs-$C_{1,2}$, and least pronounced responses (±1) were most frequently found at FAs-X. All FAs – except FAs-Y – were equally often encountered on rank ±2.

Besides regime/ conduct impact, examination of most/ least pronounced responses for **individual comportment parameters** to some extent revealed response ‘preferences’ for each group of FAs: The parameters increased ‘scattering’ (mainly during-visit), ‘vigilance’, ‘occurrence of headshakes’ (do.), ‘posture changes’, and ‘heart rate’ (do.), for instance, were most prominently affected in FAs-Y, while increased breeding (do.), agonistics, and occurrence of headshakes dominated most pronounced responses in FAs-$C_{1,2}$.

Following, results are presented in detail.

Visual appraisal offered the unique opportunity to examine **changes in overall comportment** as well as for ‘isolated parameters’. Given the substantial degree of differentiation found in Adélie penguin behavioural repertoire, it seemed reasonable to assume responses to range across various parameters rather than to concentrate on a chosen few[51].

Therefore, regime differences for a given visiting stage/ post-visit interval were examined by taking FA-proportions from the proportional-change tables in sections 5.3.1.3 to 5.3.1.11, and ranking **response magnitudes** (tab. 5.3.1-49, tab. 5.3.1-50) found in **each** comportment **parameter**.

Rank orders were established as follows: Most pronounced responses received **rank 4,** and **rank 1** was assigned to **least** pronounced responses. To distinguish between increases (+) and decreases (-) in comportment, rank positions were supplied with the respective symbols, i.e., rank +4 indicated the most pronounced increase, and rank -4 the most pronounced decrease. Ties (identical values) were accommodated by assigning the higher rank to those involved, and leaving the following rank positions empty (e.g., +4, +4, +2, +1).

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[50] Due to rarity of occurrence, comfort behaviour had not been examined separately for each regime and thus does not feature here.

[51] although that would undoubtedly be preferable for researchers…

To examine penguin overall responses, **summed rank positions across all parameters** (tab. 5.3.1-51) and **sums of most/ least pronounced responses per parameter** irrespective of ranking order (i.e., how often penguins subjected to a given regime were found on ranks ±4, ±3, ±2, and ±1, resp.; tab. 5.3.1-52) were utilised. All these helped gauge the consistency of response of penguins subjected to the same regime (key question: How many penguins do respond?).

Tables 5.3.1-49 and 5.3.1-50 summarise graded responses tallying with hypothesised severity of regime or differential visitor conduct per visiting stage (during visitation) and per post-visit interval (after visitation), respectively. Following, table 5.3.1-51 displays summed up rank positions across all comportment parameters, and table 5.3.1-52 gives an overview with respect to sums of most and least pronounced responses for each comportment parameter examined.

During visitation (tab. 5.3.1-49), graded responses were observed in each visiting stage except the very shortest (visitor approach to 3 m; lasting only a couple of seconds). Gradation was never found for all parameters together; and never with respect to agonistic behaviours.

Table 5.3.1-49: Graded Responses to Human Visitation Tallying With Hypothesised Differences in Severity of Visiting Regime as Observed for Each Visiting Stage during Human Visitation. Red entries signify differential responses to visitor conduct rather than graded response to all regimes. Param.: comportment parameter; –: decreased as compared to pre-visit; +: increased as compared to pre-visit; Sctt: Scattered Behaviour, R: Resting, B: Breed, V: Vigilance, H: Headshakes, P: Posture Changes, HR: Heart Rate; -4 to -1: decreases ranked from most to least pronounced, +1 to +4: increases ranked from least to most pronounced, 0: no change observed, n.a.: no proportion available (due to low number of sessions). FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

Visiting Stage	Param.	-4	-3	-2	-1	0/ n.a.	+1	+2	+3	+4
Visitor approach to 15m	R-	Y	B_1	$C_{1,2}$	X					
	V+						$C_{1,2}$	X	B_1	Y
	P+					$C_{1,2}$		X	B_1	Y
	HR+						$C_{1,2}$	B_1	X	Y
Visitor at 15m	Sctt+						$C_{1,2}$	B_1	X	Y
	R-	B_1	Y	X	$C_{1,2}$					
	V+						$C_{1,2}$	X	B_1	Y
Visitor approach to 5m	H+					$C_{1,2}$		B_1	X	Y
	HR+						$C_{1,2}$	X	B_1	Y
Visitor at 5m	Sctt+						X	$C_{1,2}$	B_1	Y
	P+						$C_{1,2}$	X	Y	B_1
Visitor approach to 3m	none									
Visitor at 3m	V+						$C_{1,2}$	X	B_1	Y
	HR+						$C_{1,2}$	X	B_1	Y
Visitor retreat	Sctt+						$C_{1,2}$	B_1	X	Y
	B+						$C_{1,2}$	X	B_1	Y
	HR+					Xn.a.		$C_{1,2}$	B_1	Y
Mean during-visit	HR+					Yn.a.		$C_{1,2}$	X	B_1

The greatest 'parallelism' (**four** corresponding parameters) was encountered at the initial 'presentation' of stimulus ('visitor approach to 15 m'), with regime-graded responses in increased vigilance, posture changes and heart rate. At this visiting stage, decreased resting behaviour corresponded to visitor conduct (separating loud and fast from silent and slow regimes). Responses in **three** of the eight parameters examined occurred during the stages 'visitor at 15 m' (increased scattering, and increased vigilance; decreased rest again conduct-graded) as well as during visitor retreat (increased scattering, breeding and heart rate). Graded responses for **two** comportment parameters were found during each of the stages of visitor approach to 5 m (increased occurrence of headshakes and increased heart rate), 'visitor at 5 m' (increased scattering and posture changes, both conduct-graded) and 'visitor at 3 m' (increased vigilance and heart rate).

Mean during-visit values revealed a graded response with respect to **one** parameter (heart rate) only.

After visitation (tab. 5.3.1-50), the greatest 'parallelism' (**four** corresponding parameters) was found at the initial absence of stimulus, viz., during the first post-visit interval, with regime-graded responses in increased vigilance and heart rate , and with conduct-graded responses in increased breeding and posture changes. Responses in **three** of the eight parameters occurred in the last post-visit interval (decreased rest, increased posture changes and heart rate). The second (increased vigilance and posture changes) and fourth (increased scattering and conduct-graded increased heart rate) post-visit intervals each contained graded responses with respect to **two** parameters, while the third post-visit interval was the only one for which a graded response was observed in **one** parameter only (decreased resting).

Mean post-visit values revealed graded response for **four** parameters, viz., decreased rest, increased vigilance, increased posture changes, and increased scattering (conduct-graded).

Table 5.3.1-50: Graded Responses to Human Visitation Tallying With Hypothesised Differences in Severity of Visiting Regime as Observed for Each of Five Post-Visit Intervals after Human Visitation. Red entries signify differential responses to visitor conduct rather than graded response to all regimes. Post-Vis Int: post-visit interval; Param.: comportment parameter; –: decreased as compared to pre-visit; +: increased as compared to pre-visit; Sctt: Scattered Behaviour, R: Resting, B: Breed, V: Vigilance, H: Headshakes, P: Posture Changes, HR: Heart Rate; -4 to -1: decreases ranked from most to least pronounced, +1 to +4: increases ranked from least to most pronounced, 0: no change observed, n.a.: no proportion available (due to low number of sessions). FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

Post-Vis Int	Param.	-4	-3	-2	-1	0/ n.a.	+1	+2	+3	+4
1 (1-2 min)	B+					X		$C_{1,2}$	B_1	Y
	V+						$C_{1,2}$	X	B_1	Y
	P+						X	$C_{1,2}$	Y	B_1
	HR+					Xn.a.		$C_{1,2}$	B_1	Y
2 (3-4 min)	V+						$C_{1,2}$	B_1	X	Y
	P+						$C_{1,2}$	X	B_1	Y
3 (5-6 min)	R–	X	B_1	$C_{1,2}$		Yn.a.				
4 (7-8 min)	Sctt+						$C_{1,2}$	B_1	X	Y
	HR+					X		$C_{1,2}$	Y	B_1
5 (9-10 min)	R–	B_1	X	$C_{1,2}$		Yn.a.				
	P+					Yn.a.		$C_{1,2}$	X	B_1
	HR+					$C_{1,2}$		B_1	X	Y
Mean post-visit	Sctt+						X	$C_{1,2}$	Y	B_1
	R–	Y	B_1	X	$C_{1,2}$					
	V+						$C_{1,2}$	B_1	X	Y
	P+						$C_{1,2}$	X	B_1	Y

Overall sums of ranked responses (in tab. 5.3.1-51, row: tot) make a good case for regime-and/or conduct-mediated gradation of responses, but again show that no single regime could claim a consistent rank. **During** visitation (row: dur), FAs-Y (regime 3 P, L&F) most often held rank ±4 (most pronounced response, 32 times), while FAs-B_1 (regime 1 P, L&F) were most often found on the subsequent rank (±3; 33 times); FAs-X most frequently occupied rank ±2 (33 times), and FAs-$C_{1,2}$ were predominantly found on the least pronounced rank position (±1; 41 times). **Post-**

visit (row: post), however, most pronounced responses (±4) were most often found at FAs-B_1 (21 times), though they remained prominent at FAs-Y (15 times), and least pronounced responses at FAs-X (22 times) while highest number of ranked responses for third ranks (±3) was observed at FAs-$C_{1,2}$ (17 times), and all FAs except FAs-Y (5 times) were equally often found on rank ±2 (13 times each).

Table 5.3.1-51: Ranked Responses Summed Up per Rank Position for Each Visiting Regime. Values depict sum of overall responses per rank position (tot), sum of during-visit responses (during), and sum of post-visit responses (post). ±4 to ±1: ranked from most to least pronounced, FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

	Rank ±4				**Rank ±3**				**Rank ±2**				**Rank ±1**			
FAs	Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$
tot	47	30	17	23	20	33	25	32	14	28	33	25	16	23	40	41
during	32	9	8	15	10	24	17	15	9	15	20	12	12	16	18	24
post	15	21	9	8	10	9	8	17	5	13	13	13	4	7	22	17

Focusing on the sums of **most and least pronounced responses** per visiting regime for **each comportment parameter** (tab. 5.3.1-52), it became apparent that rankings of FAs differed between parameters as well as between periods (within parameters).

During visitation (across all visiting stages), FAs-Y (regime 3 P, L&F) most often exhibited the most pronounced responses of all four regimes with respect to the parameters ‘scattering’, ‘headshakes’, ‘posture changes’, and ‘heart rate’ (all increases), additionally they were tied with FAs-B_1 with respect to ‘vigilance[52] ’. FAs-B_1 (regime 1 P, L&F) showed the most pronounced response in terms of decreased resting behaviour (tie with FAs-Y for increased vigilance), while most pronounced responses for FAs-$C_{1,2}$ (predominantly regime 1 P, S&S) were found as regards increased breeding and agonistic behaviours, and FAs-X (regime 3 P, S&S) never emerged the winner in the contest for most pronounced responses in any single comportment parameter. Complementing these findings, FAs-$C_{1,2}$ were assigned the rank of least pronounced response during visitation as regards decreased rest, increased vigilance, and increased heart rate.

After visitation (across all post-visit intervals), FAs-B_1 were found to exhibit the highest number of most pronounced responses for increased scattering, breeding, headshakes, and posture changes. FAs-Y continued to show the highest number of most pronounced responses for the parameters decreased ‘rest’ and increased ‘vigilance’, while FAs-$C_{1,2}$ and FAs-X were more often encountered displaying least pronounced responses (FAs-$C_{1,2}$: decreased rest, increased vigilance and posture changes; FAs-X: increased scattering, breeding, headshakes).

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[52] tie with FAs-B_1 during, but not post-visitation

Table 5.3.1-52: Most Pronounced and Least Pronounced Responses Summed Up for Each Comportment Parameter per Visiting Regime. Values depict sum of overall responses (tot), sum of during-visit responses (during) and sum of post-visit responses (post). Parameter: comportment parameter; –: decreased as compared to pre-visit; +: increased as compared to pre-visit; Sctt: Scattered Behaviour, R: Resting, B: Breed, V: Vigilance, A: Agonistics, H: Headshakes, P: Posture Changes, HR: Heart Rate. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F. **N.b.:** Different overall sums result from ties (e.g., both FAs B_1 and FAs-Y found on rank 1 for vigilance).

Parameter	Period	Most Pronounced				Least Pronounced			
		Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$
Sctt+	tot	8	4	2	1	1	3	6	4
	during	7	0	1	0	1	3	2	2
	post	1	4	1	1	0	0	4	2
R–	tot	4	6	5	0	3	0	3	8
	during	1	4	3	0	3	0	1	4
	post	3	2	2	0	0	0	2	4
B+	tot	3	4	1	6	2	2	10	1
	during	2	1	0	5	2	1	5	1
	post	1	3	1	1	0	1	5	0
V+	tot	7	4	4	0	0	1	0	13
	during	3	3	2	0	0	0	0	8
	post	4	1	2	0	0	1	0	5
A+	tot	3	2	2	7	5	6	7	0
	during	2	0	1	5	4	3	4	0
	post	1	2	1	2	1	3	3	0
H+	tot	6	3	1	6	2	5	6	2
	during	5	0	1	3	1	4	2	2
	post	1	3	0	3	1	1	4	0
P+	tot	7	4	1	2	1	6	3	6
	during	5	1	0	2	1	5	1	3
	post	2	3	1	0	0	1	2	3
HR+	tot	9	3	1	1	2	0	5	7
	during	7	1	0	0	0	0	3	5
	post	2	2	1	1	2	0	2	2

5.3.1.13 Section summary

N.b.: This section summary will not dwell on regime differences, as these will be presented comprehensively for all sections together at the end of chapter 5.3.

Visual appraisal was undertaken for a total of **9 comportment parameters**, comprising 7 behavioural parameters (scattered behaviour, resting, comfort, breeding, vigilance, agonistics, and occurrence of headshakes[53]), as well as posture and heart rate (tab. 5.3.1-53). (Displays had originally been included in the list of parameters, but could not be appraised due to rarity of occurrence prior to, and complete absence during as well as after human visitation.)

Responses to non-human disturbance types (including aircraft) will be summarised first, followed by findings relating to human visitation.

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[53] including ruffle-shakes (= full-body shakes), in which, after all, the head is also shaken

While all comportment parameters changed during human visitation (s.b.), only selected parameters could be considered indicative of the other **disturbance types** examined (tab. 5.3.1-53). For these, a graded response became apparent.

Conspecific ‘stationary’ presence at the focal nest did not elicit consistent responses from any of the parameters appraised, whereas conspecific movement at the focal nest frequently led to increased agonistic behaviour (19 of 40 sessions), but only rarely caused increased scattering of behaviour (1 of 45), decreased resting (2 of 45) or increased vigilance behaviour (3 of 45). These responses, in turn, were more commonly observed during bouts of increased conspecific movement irrespective of distance from the focal nest (increased scattering: 6 of 49; decreased resting: 9 of 51; increased vigilance: 15 of 51).

N.b.: In combination with the Conspecific Movement Measure, which had indicated higher conspecific movement at FAs-C$_{1,2}$ prior to visitation, a less pronounced response to human visitation (less difference from pre-visit values) would thus be expected with respect to the comportment parameters ‘scattered behaviour’, ‘resting’, ‘vigilance’, and, possibly[54], ‘agonistics’.

Table 5.3.1-53: Overview of Nine Comportment Parameters for Which Responses Towards Different Types of Disturbance Were Appraised. For human visitation, mean proportional values for the entire periods (during and post, resp.) are presented. For conspecific, skua, and aircraft disturbance, number of sessions during which response was observed is given in relation to total number of sessions for which disturbance parameter was present (xx of yy). H_dur: during human visitation, H_post: after human visitation; C_stat. at nest: conspecific ‘stationary’ presence at focal nest, C_move at nest: conspecific movement at the focal nest, C_move irresp. d: conspecific movement irrespective of distance to the focal nest; SLOF: skua low overflight, Skua-G: skua on ground and close to the focal nest; Aircraft: aircraft noise; +: increase, –: decrease; Sctt: Scattered Behaviour, R: Resting, C: Comfort, B: Breed, V: Vigilance, A: Agonistics, H: Headshakes, P: Posture Changes, HR: Heart Rate. Colours correspond to change classes, and grey-scale follows the same code as coloured cells (proportions in tab. 5.3.1-7).

	Sctt+	R–	C+	C–	B+	V+	A+	H+	P+	HR+
H_dur	27 %	-63 %	8 %	-24 %	16 %	56 %	16 %	21 %	17 %	37 %
H_post	31 %	-40 %	24 %	-25 %	22 %	34 %	15 %	29 %	19 %	19 %
C_stat. at nest	0 of 33	1 of 33	no response in either direction		0 of 28	0 of 33	3 of 30	0 of 31	0 of 30	0 of 18
C_move at nest	1 of 45	2 of 45			0 of 39	3 of 45	19 of 40	0 of 42	0 of 40	0 of 27
C_move irresp. d.	6 of 49	9 of 51			0 of 43	15 of 51	3 of 43	0 of 45	1 of 44	3 of 32
SLOF	1 of 13	5 of 13	ditto		1 of 13	6 of 13	0 of 12	2 of 13	1 of 14	0 of 8
Skua-G	0 of 5	4 of 5			0 of 3	5 of 5	3 of 4	0 of 5	0 of 6	1 of 3
Aircraft	0 of 3	0 of 3	ditto		0 of 3	3 of 3	0 of 3	0 of 3	0 of 3	0 of 1

Skua low overflights frequently caused increased vigilance (6 of 13) as well as reductions in resting behaviour (5 of 13 sessions), but only rarely coincided with increased occurrence of headshakes (2 of 13), or increased occurrence of posture changes (1 of 14); increased scattering (1 of 13), or increased breeding (do.). Skua presence on the ground and close to the focal nest was always accompanied by increased vigilance (5 of 5). It nearly invariably resulted in reduced resting behaviour (4 of 5) and increased agonistic behaviour (3 of 4), while it led to increased heart rate only once (1 of 3).

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[54] CMM did not differentiate distance from the focal nest, i.e., conspecific movement close to the FA was included but its extent was not separately evaluated.

With respect to the few occurrences of **aircraft noise**, an increase in vigilance was invariably observed (3 of 3 sessions), whereas none of the other comportment parameters changed.

For the following statements pertaining to **human visitation**, the reader is referred to tables 5.3.1-6 and 5.3.1-7.

Prior to human visitation, predominant resting behaviour was frequently observed (mean pre-visit FAs-allReg: 40 %; third proportional class), whereas predominant vigilance behaviour was rare (14 %; lowest prop. class). Of all the comportment parameters for which occurrence had been appraised (i.e., not for resting and heart rate), only occurrence of vigilance behaviour was very frequent (76 %; highest prop. class). Breeding (41 %), agonistic (40 %), and scattered behaviour (32 %) occurred frequently. Headshakes were infrequently observed (17 %; second prop. class), while posture changes (12 %) and comfort behaviour (11 %) were found to rarely occur in the sessions included in the appraisal procedure. Heart rate was most frequently appraised as ‘undulating regularly’ (82 %; highest prop. class).

During and after human visitation (as compared to pre-visit), increases constituted the main direction of change for heart rate and posture changes as well as for most behaviours (scattered behaviour, breeding, vigilance, and agonistic behaviour, occurrence of headshakes). Resting behaviour was the only comportment parameter for which distinct decreases were observed, while increases and decreases were found with respect to comfort behaviour.

Findings indicate that **human visitation** caused focal animals to substantially alter their overall comportment **during** the visit itself. Furthermore, they suggest that focal-animal responses tended to persist well **beyond the end** of human visitation (tab. 5.3.1-53).

During visitation, changes (as compared to pre-visit) were observed in all comportment parameters (tab. 5.3.1-54); change classes occupied ranged from highest (75 % and above) to second lowest class (15 % to 29 %).

Maximum changes in at least 75% of all sessions appraised (highest change class for all FAs together) were calculated for decreased resting behaviour (-85 %), increased vigilance behaviour (+81 %), and increased heart rate (+80 %). Increases in approximately half of all sessions (change class 45 % to 59 %) were found for scattered behaviour (+46 %), while increases in occurrence of headshakes (+44 %), occurrence of posture changes (+39 %), breeding (+35 %) and agonistic (+33 %) behaviour could all be assigned to the third change class (30 % to 44 %). As for changes in comfort behaviour, both increases (+21 %) and decreases (-29 %) fell into the second change class (15 % to 29 %).

Antidirectional changes (examined per visiting stage for all FAs together; tabs. 5.3.1-16, 5.3.1-28, and 5.3.1-44) between visitor approach to 15 m and visitor retreat, predominantly grouped decreased resting with increased vigilance (Σ all stages: 210 times) and increased heart rate (Σ all stages: 65 times). Between the stages ‘visitor at 15 m’ and ‘visitor retreat’, decreased resting behaviour was additionally frequently accompanied by increased agonistic (Σ all stages: 45 times) and breeding behaviour (Σ all stages: 37 times).

Syndirectional changes (examined per visiting stage for all FAs together; tabs. 5.3.1-29, and 5.3.1-45) between visitor approach to 15 m and visitor retreat mainly concerned increased vigilance in conjunction with increased heart rate (Σ all stages: 60 times), occurrence of headshakes (Σ all stages: 47 times), posture changes (Σ all stages: 39 times), and agonistics (Σ all stages: 31 times). From the stage ‘visitor at 15 m’ onwards, increased vigilance was additionally frequently accompanied by increased breeding behaviour (Σ all stages: 26 times).

Table 5.3.1-54: Overview of Focal Animal Responses by Visiting Stage. Only the 2 highest values for each comportment parameter have been included (FAs-allReg). Highest values are underscored. Proportions based on less than 5 sessions have been omitted (thus, no values for comfort behaviour shown). %: proportion of response, n_{tot}: total number of sessions; +: increase as compared to pre-visit, –: decrease as compared to pre-visit; Sctt: Scattered Bbehaviour, R: Resting, B: Breed, V: Vigilance, A: Agonistics, H: Headshakes, P: Posture Changes, HR: Heart Rate. Colour code follows tab. 5.3.1-7.

Visiting Stage	Parameter	%	n_{tot}
Visitor Along Colony (20 m – 25 m) Pre-Visit	no highest/ second highest values		
Visitor Approach to 15 m	no highest/ second highest values		
Visitor at 15 m	no highest/ second highest values		
Visitor Approach to 5 m	HR+	80	25
Visitor at 5 m	Sctt+	46	46
	B+	35	40
	P+	39	44
	R–	-83	48
	V+	75	48
	H+	38	42
Visitor Approach to 3 m	A+	29	41
	HR+	62	26
Visitor at 3 m	R–	-85	48
	V+	81	48
	A+	33	39
	H	44	43
	Sctt+	43	47
	B+	25	40
	P+	27	44
Visitor Retreat	no highest/ second highest values		
Visitor Along Colony (20 m – 25 m) Post-Visit	no highest/ second highest values		

The **visiting stages** that encompassed the greatest changes in comportment (highest or second highest proportional values for each comportment parameter; tab. 5.3.1-54) were those from and including visitor approach to 5 m to and including visitor stay at 3 m. Heart rate response, however, preceded behavioural responses in that the highest proportional value for increased heart rate was assigned to the stage of visitor approach to 5 m. As the second highest value for heart rate increases fell into the stage of approach to 3 m, it is suggested that focal-animal heart rate was more sensitive to stimuli moving towards the birds than to stimuli remaining at a stable distance.

After visitation, changes (as compared to pre-visit) were likewise observed in all comportment parameters (tab. 5.3.1-55), but rarely attained change classes comparable to those occupied during visitation; change classes ranged from fourth (45 % to 59 %) to second lowest class (15 % to 29 %).

Maximum changes (FAs-allReg) were of substantially smaller magnitude than during visitation with respect to increased heart rate (+25 %; drop by four, from highest to second change class), decreased resting (max. post-visit value: -47 %; drop by two, from highest to fourth change class), and increased vigilance (+43 %; do.[55]). They were of considerably smaller magnitude for scattered behaviour (+38 %, drop by one, from fourth to third change class), posture changes (+28 %, drop by one, from third to second change class), and agonistic behaviour (+19 %, do.). Little alteration in magnitude of change values was found for maximum values obtained for breeding behaviour (post-visit: +31 % vs. during-visit: +35 %, both third class), and no change was observed as regards

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[55] for German readers: ditto (dt.: dto.)

maximum values calculated for occurrence of headshakes (+44 %, do.). With respect to comfort behaviour, post-visit maximum values for increased occurrence were higher than the respective during-visit values (post-visit: +46 % vs. during-visit: +21 %[56], drop by two, from fourth to second class), while values for decreases remained approximately equal (-31 % vs. -29 %[57]; just 'crossing' the border from third to second class).

Antidirectional changes (examined per post-visit interval for all FAs together; tabs. 5.3.1-18, 5.3.1-31, and 5.3.1-47) predominantly grouped decreased resting with increased vigilance (Σ all intervals: 73 times), but the opposite conjunction became increasingly more common during the post visit-period (Σ all intervals: 35 times). Decreased resting behaviour additionally frequently coincided with increased breeding (Σ all intervals: 35 times). To a lesser extent, it was observed in conjunction with increased agonistic behaviour (Σ all intervals: 15 times), increased heart rate (Σ all intervals: 15 times), and increased comfort behaviour (Σ all intervals: 13 times).

Syndirectional changes (examined per post-visit interval for all FAs together; tabs. 5.3.1-32, and 5.3.1-48) mainly concerned increased vigilance in conjunction with increased occurrence of headshakes (Σ all intervals: 35 times), breeding (Σ all intervals: 24 times), posture changes (Σ all intervals: 21 times), and – to a much lesser extent with increased agonistics (Σ all intervals: 12 times), increased heart rate (Σ all intervals: 11 times), and increased comfort behaviour (Σ all intervals: 9 times).

The greatest changes in comportment (highest or second highest proportional values for each comportment parameter; tab. 5.3.1-55) were found during the first three **post-visit intervals**

Table 5.3.1-55: Overview of Focal Animal Responses in the Five 2 min-Intervals after Human Visitation. Only the 2 highest values for each comportment parameter have been included (FAs-allReg). Highest values are underscored. Proportions based on less than 5 sessions have been omitted (thus, only one value for comfort behaviour shown). %: proportion of response, n_{tot}: total number of sessions; +: increase as compared to pre-visit, –: decrease as compared to pre-visit; Sctt: Scattered Behaviour, R: Resting, C: Comfort, B: Breed, V: Vigilance, A: Agonistics, H: Headshakes, P: Posture Changes, HR: Heart Rate. Colour code follows tab. 5.3.1-7.

Post-Visit Stage	Parameter	%	n_{tot}
1-2 min Post-Visit	R–	-47	51
	A+	19	42
	H+	44	45
	HR+	25	24
	Sctt+	37	49
	V+	41	51
3-4 min Post-Visit	Sctt+	38	47
	V+	43	49
	R–	-43	49
	B+	22	41
	P+	23	43
5-6 min Post-Visit	C+	46	13
	B+	31	39
	P+	28	43
	A+	18	39
	H+	33	39
7-8 min Post-Visit	HR+	20	30
9-10 min Post-Visit	no highest/ second highest values		

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[56] value not shown in tab. 5.3.1-54, due to being based on less than 5 sessions

[57] values not shown in tabs. 5.3.1-54 and 5.3.1-55, due to being based on less than 5 sessions

(1-6 min). Not all comportment parameters exhibited the same pattern so that highest values were found in each of these intervals: For decreased rest, increased agonistics, occurrence of headshakes, and increased heart rate, they fell into the first (1-2 min), while highest values for increased scattering and vigilance were calculated for the second (3-4 min), and those for increased comfort and breeding behaviour as well as for increased posture changes occupied the third post-visit interval (5-6 min).

Second highest values[58] pointed to an initial rising of response with respect to scattered behaviour and vigilance (preceding highest values found in the second post-visit interval), and for breeding behaviour and posture changes (preceding highest values found in the third post-visit interval). Resting behaviour was the only comportment parameter to exhibit a successive waning of response, with the second highest value immediately following the highest. A decreasing response level with slight fluctuations was found with respect to increased agonistic behaviour and increased occurrence of headshakes. The pattern for increased heart rate was unusual in that the second highest value[59] was calculated for the fourth post-visit interval (7-8 min).

While these findings indicate a relative recovery within the post-visit period, it should be kept in mind that for all of the comportment parameters examined, proportions 10 min post-visit (see respective tables for each comportment parameter) suggest that at least for some birds, this time was not sufficient to recuperate and return to the comportment exhibited prior to visitation.

5.3.1.14 Questions Arising from Visual Appraisal

Results from visual appraisal raised the following questions which will be quantitatively examined in the following sections.

1. Does the overall time spent in a specific behaviour system/ posture change during and/or after human visitation? Do regime differences become apparent? → Addressed in section 5.3.2.1
2. Does heart rate variation change during and/or after human visitation? How does this change compare to ‘natural fluctuations’ over a similar interval of time outside visitation (‘baseline’ sessions)? → Addressed in section 5.3.2.2
3. Does the duration of phases of behaviour systems/ postures/ heart rate categories change during and/or after human visitation; if so, which behaviour systems/ postures/ heart rate categories are subjected to increases/ decreases in phase duration? Do regime differences become apparent? → Addressed in section 5.3.3

Does the frequency of occurrence per period of behaviour & heart rate phases/ posture states change during and/or after human visitation; if so, does this concern all behaviour systems/ postures/ heart rate categories alike, or are there specific behaviour systems/ posture states/ heart rate categories subjected to increases/ decreases in frequency of occurrence? Do regime differences become apparent? → Addressed in section 5.3.3

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[58] With respect to comfort behaviour, only the highest value is shown as proportion for the second highest (second post-visit interval; 3-4 min) was based on 4 sessions only

[59] highest in 1st post-visit interval

5.3.2 Quantitative Comparisons

Analyses of behaviour systems and the posture ‘prone’ were complemented by quantitative comparison of heart rate variation in ‘visited’ and ‘baseline’ sessions using a number of (descriptive) statistical parameters (see section 5.3.2.2).

5.3.2.1 Prevalence of Behaviour Systems and Postures Exhibited before, during, and after Human Visitation

Following qualitative visual appraisal and quantitative assessment of consistency of responses among focal animals (key question: How many?), quantitative comparison of prevalence of behaviour systems and one of the two mutually exclusive postures examined magnitudes of between-period changes in proportional occurrence of each parameter before, during, and after human visitation (key question: How much?).

Data presented on behaviour and posture are based on 51 sessions (from 19 FAs) in the course of which human visitation had taken place (tab. 5.3.2-1).

Table 5.3.2-1: Database used for Quantitative Comparison of Prevalence of Behaviour Systems and Postures. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

	FAs-allReg	FAs-B_1	FAs-$C_{1,2}$	FAs-X	FAs-Y
Number of Sessions	51	17	16	12	6
Number of FAs	19	5	5	5	4

N.b.: Since the impression of scattered behaviour is generated by quick succession of several systems, it does not appear in this section (cf. chapter 5.3.1, Visual Appraisal). Within the behaviour system of comfort, shakes were again evaluated separately. As during visual appraisal, the *term headshake* is used generically and *includes ruffle-shakes* – in which, after all, the head is also shaken.

5.3.2.1.1 Methodological Prelude

Recapitulation: Primary transcriptions had served to unite information collected by various media (video, data logger, field notebook) in hard-copy transcription matrices (paper). They had yielded a second-by-second account of focal animal behaviour elements and posture, conspecific presence, actions and distance, as well as human visitation (conduct, number, distance).

- **Secondary Transcriptions of Focal-Animal Behaviour, Posture, and Human Disturbance**

For secondary transcriptions, the Excel-sheets created for Visual Appraisal (q.v.) were used: Time (in seconds) spent in each of the behaviour systems (i.e., performing behavioural elements assigned to that system) was summed up per period (pre-visit, during-visit, post-visit), divided by the duration of the period, and multiplied by 100. Time spent ‘prone’ (lying) was treated likewise.

The Visiting Stage Performance Indicator Value (q.v.; tab. 5.3.1-3) introduced in the previous section served to distinguish the period of visitation from periods before and after the visit.

Conspecific and **predator/ aircraft** disturbance do not feature in this section.

■ Presentation of Results

Tabulated results: Using Friedman-tests, consistency of directions of change was examined for FAs from ***all visiting regimes*** together.

Figures: Boxplots were drawn to visualise period differences in each parameter with respect to ***individual visiting regimes***.

Colour code: The colour code used to facilitate visual discrimination of significance levels has been introduced in the chapter Materials and Methods (tab. 4-20).

In the following subsections, **verbalisation of tabulated results** as well as presentation of boxplots is provided separately for each comportment parameter. In the text, proportions = 1 % are rounded off, while exact proportions are given for values < 1 %.

N.b.: Two similar-sounding **key values** will be reported for each parameter. These values are derived from the same mathematical procedures (subtraction and calculation of median), but as these were employed in different order, the values reflect different foci:

The key value <u>difference in (period) medians</u> (DiM) represents the median of one period subtracted from that of another period (1. calculation of median, 2. subtraction). It constitutes the **overall difference** found at ***all regimes*** together and at ***individual regimes***, respectively.

DiM for ***all regimes*** can be calculated from tabulated median values presented at the beginning of each subsection (e.g., tab. 5.3.2-6): This is effected by subtracting pre- from during-visit values, during- from post-visit values, and pre- from post-visit values, respectively. For ***individual regimes***, they are presented in the text and tabulated in appendix 5.3.2-3.05.

Example – Difference in (Period) Medians (DiM):

Median proportion for resting behaviour **pre-visit** = 60.70 %

Median proportion for resting behaviour **during-visit** = 21.10 %

The <u>difference in medians</u> amounts to -39.60 % (reported as -40 %, the minus indicating a decrease from pre- to during-visitation).

In contrast, <u>median of differences</u> (MoD) key values are based on differences between periods found within each session, i.e. proportions of one period are subtracted from that of another. The median is then calculated across these between-period values (1. subtraction, 2. calculation of median). MoD-values thus represent a **measurement of response magnitude** (from pre- to during-visitation) as well as on the **magnitude** of post-stimulus **waning of responses** (from during- to post-visitation) observed in individual sessions. With respect to differences between pre- and post-visitation, they provide an insight into the **extent of recovery** found within each session (the smaller the deviation, the greater the similarity between behaviour prior to and after visitation).

Median-of-differences values based on FAs of ***all regimes*** are presented at the beginning of each subsection (e.g., tab. 5.3.2-6). For FAs subjected to ***individual regimes***, they are given in the text and tabulated in appendis 5.3.2-3.06.

Example – Median of Differences (MoD):

The difference in proportions of resting behaviour pre-visit vs. during-visit amounted to

FA B3-1 on 24.11.2000 = +9%

FA B3-2 on 17.11.2000 = -70 %

FA C1-1 on 26.11.2000 = -4 %

FA X 2-1 on 24.11.2001 = -34 %

FA Y5-2 on 01.12.2001 = -83 %

etc. for all 51 sessions/ for all sessions of a given regime.

The median of differences key value is calculated from these values.

Order of Presentation: To provide a first overview, results on ‘among’-period differences (among all three periods) for all regimes together (global Friedman-test; tab. 5.3.2-3), and on between-period directions of change for individual regimes (tab. 5.3.2-4; tab. 5.3.2-5) are presented jointly for **all behaviour and posture parameters** together (section 5.3.2.2.3). Tabulated results on individual sessions are found in appendix 5.3.2-1.

Subsequently, the following **order of presentation** has been adopted for ***each behaviour system, headshakes and posture***: After a brief description of the pre-visit ‘status quo’ (presented for all regimes and each regime), results on **directions of change** (overall differences) **among** the **periods** (pre-visit, during-visit, post-visit) are followed – if applicable, i.e., if global Friedman-test indicated significant differences among periods – by those on pair-wise comparisons.

Within each of these ‘packages’, the main effect is presented first for ***all regimes*** together (Friedman-tests), followed by results on ***individual regimes*** (boxplots) and ***individual sessions*** (appendix 5.3.2-3.01 and -3.02).

Presence of lesser effects ‘strikingly’ different from the overall effect is subsequently mentioned if applicable.

N.b.: In boxplots, Y-axes have been scaled to suit each behaviour system/ posture so that care must be taken when comparing across comportment parameters.

With respect to **pair-wise comparisons**, the difference between **pre- and during**-visit proportions is considered to reflect the immediate effect of visitation, while the difference between **during- and post**-visit proportions is suggested to shed light on the focal animals’ continuing/ waning response after withdrawal of the stimulus. The difference between **pre- and post**-visit proportions thus gives an indication as to the extent to which the animals have managed or failed to achieve recovery during the post-visit period.

5.3.2.1.2 Interim Summary – Results on Prevalence of Behaviour Systems and Postures

N.b.: Differences ***individual regimes*** will be comprehensively presented at the end of the chapter summary (5.3.4).

Summing up, this section set out to address the question whether the prevalence, i.e., overall time spent in a specific behaviour system/ posture changed during human visitation.

Behavioural and postural responses as detected by quantitative changes in prevalence yielded the following results:

For ***all regimes*** together, global Friedman-test detected significant **among-period differences** (among all three periods) with respect to resting and vigilance behaviour, as well as for time spent performing headshakes and time spent 'prone'. Overall differences were not significant for the comportment parameters 'comfort', 'breed', and 'agonistics' (and, consequently, no follow-up pair-wise Friedman-tests were performed).

As regards **between-period differences** (between two periods) for ***all regimes***, pair-wise Friedman-test indicated significant decreases from **pre- to during-visitation** for the parameters 'rest' and 'posture: prone', while significant increases were detected for the parameters 'vigilance' and 'headshakes'.

With respect to <u>response directions</u> in ***individual sessions***, resting behaviour and time spent 'prone' decreased in the majority of sessions (rest: 48 of 51 sessions = 94 %; 'prone': 28 of 51 sessions = 55 %), whereas vigilance behaviour (92 %), time spent performing headshakes (59 %), agonistic behaviour (55 %), and breeding behaviour (53 %) increased in the majority of sessions. With respect to comfort behaviour, 'no change' was observed more often (43 %) than increases (37 %) which, in turn, were more common than decreases (20 %). The category 'no change', however, invariably contained sessions of 'continuing absence', i.e., comfort behaviour had been entirely absent prior to visitation. For the other behaviours, 'no change' between pre- and during-visit proportions likewise indicated in the majority of cases that the behaviour had not been shown prior to visitation and continued not to be exhibited during the visit.

The <u>magnitude</u> of within-session <u>response</u> across all sessions was most pronounced with respect to increased vigilance (<u>median of differences</u>: +32 %) and decreased resting behaviour (MoD: -30 %), indicating that the greatest changes were observed in these behaviours.

Range-values for all behaviours, however, showed great fluctuations, pointing to distinct individual responses partly dependent on behavioural repertoire exhibited prior to visitation (e.g., for breeding and comfort: higher proportions pre-visit more likely to be reduced during-visit; for agonistic behaviour: higher proportions pre-visit more likely to further increase during-visit).

Looking at changes from **during- to post-visitation**, significant changes for ***all regimes*** (Friedman-test) comprised an increase in resting behaviour and a decrease in vigilance behaviour. Changes observed in the parameter 'posture: prone' were only tendentially significant; changes in the parameter 'headshakes' as well as in the remaining parameters did not attain statistical significance.

With respect to <u>response directions</u> in ***individual sessions***, resting behaviour increased in the majority of sessions (40 of 51 sessions = 78 %), whereas vigilance behaviour (92 %) decreased in the majority of sessions. Time spent 'prone' increased in 53 % of all sessions, while decreases were observed with respect to time spent performing headshakes (51 %). Breeding behaviour was almost equally likely to increase (51 %) or decrease (49 %), while agonistic behaviour decreased in 47 % of all sessions.

'No change' between during- and post-visit proportions (found particularly often with respect to comfort behaviour) generally indicated that the behaviour had not been shown during visitation and continued not to be exhibited afterwards.

The response <u>magnitude</u> of within-session <u>response</u> across all sessions was most pronounced with respect to decreased vigilance (<u>median of differences</u>: -31 %) and increased resting behaviour

(MoD: +20 %), indicating that the greatest changes were again observed in these behaviours. While median change in vigilance behaviour was similar in magnitude to that observed previously (from pre- to during: +32 %), it was far less pronounced for resting behaviour (from pre- to during: -30 %) so that the remaining behavioural parameters jointly attained a greater prominence after visitation (by ‘filling up the difference’).

Range values were again substantial.

Statistical comparison of **post-** and **pre-visit** proportions for ***all regimes*** depicted **recovery** to have been more or less effected for all comportment parameters examined (with pair-wise Friedman-test significances being low, tendential, or non-existent).

The inspection of ***individual sessions***, however, suggested **divergent post-visit comportment** to be at least partly responsible for the statistical result obtained: Table 5.3.2-2 indicates that for each parameter, the majority of post-visit responses either constituted an **incomplete return** to (IR; behaviour deviating in the same direction as during visitation, only less so), or an **‘overshooting’** of pre-visit levels (O; behaviour altered antidirectionally to during-visitation, and more pronounced than pre-visit), but rarely represented a ‘true’ recovery.

‘Strategies’ for dealing with post-stimulus recovery thus appeared to be more variable than the immediate response to said stimuli.

Table 5.3.2-2: Divergent Post-Visit Comportment May Partly Obscure Existing Failure to Achieve Recovery. Pair-wise Friedman-test results on overall differences between pre-visit and post-visit periods are compared to proportions of individual sessions for which post-visit behaviour was lower/ higher/ the same as pre-visit behaviour. χ^2: Friedman-test statistic; *: significant, $^{(*)}$: tendentially significant; n.s.: pair-wise Friedman-test not significant (after significant global Friedman-test), n.a.: global Friedman-test = n.s. → no pair-wise Friedman-test performed; IR: incomplete return = behaviour deviating in the same direction as, but less pronounced than during visitation; O: overshooting = behaviour altered antidirectionally to during-visitation, and more pronounced than pre-visit. Σ: sum of proportions lower and higher than pre-visit.

comportment parameter	χ^2-value (pre-visit vs. post-visit)	% post-visit lower than % pre-visit	% post-visit higher than % pre-visit	Σ % post-visit different from % pre-visit	% post-visit same as % pre-visit
rest	3.314$^{(*)}$	63 % - IR	37 % - O	100 %	0 %
comfort	n.a.	22 % - O	39 % - IR	61 %	39 %
breed	n.a.	41 % - O	55 % - IR	96 %	4 %
vigilance	3.920*	35 % - O	63 % - IR	98 %	2 %
agonistics	n.a.	43 % - O	47 % - IR	90 %	10 %
headshakes	4.333*	25 % - O	51 % - IR	67 %	24 %
posture: 'prone'	(1.778) n.s.	43 % - IR	27 % - O	70 %	30 %

This result is only partly reflected in magnitudinal values (magnitude of within-session response across all sessions; e.g., for rest: median of differences = -10 %, for vigilance: MoD = +8 %, but low to nonexistent for other behaviours). Range-values (span from min. to max.) for all behaviours, however, were substantial (e.g., for rest: -93 % to +44 %; for comfort: -67 % to +78 %; for breed: -18 % to +57 %; for vigilance: -35 % to +57 %), pointing to the persisting individuality of post-stimulus responses and, ultimately, recovery.

Following, results are presented in detail.

5.3.2.1.3 Directions of Change among Periods

Without regard to continuity and frequency of occurrence (section 5.3.3; q.v.), the **proportion of time** allocated to each behaviour system, to headshakes, and to the posture 'prone' was compared for the periods before, during, and after human visitation. Proportions were used to facilitate comparisons and account for differing period durations. For each period (pre, dur, post), all behaviour systems and time spent performing headshakes added up to 100 %. As summation of proportions of the two postures 'prone' and 'up' likewise yielded 100 % (cf. tab. 5.3.2-5), only one was analysed.

At first, 'among'-period differences (i.e., among all three periods) for ***all regimes*** together were analysed using global Friedman-tests (Friedman-test statistic: χ^2). If applicable, i.e., if significant differences among the periods had been obtained, these were followed by Friedman pair-wise tests between two periods (pre-visit vs. during-visit, during-visit vs. post-visit, pre-visit vs. post-visit; table 5.3.2-3). Global Friedman-tests detected significant results with respect to the parameters 'rest', 'vigilance', 'headshakes' and 'posture_prone'. Results on the follow-up pair-wise Friedman-tests are presented in detail in the parameter-specific subsections.

Table 5.3.2-3: Friedman-Test Results for Quantitative Changes in Behaviour Systems, Headshakes, and Posture. FA: focal animal; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y); pre: before visitation, dur: during visitation, post: after visitation; χ^2-value: Friedman-test statistic, *p*: significance level. Significant values are underscored. *Italics* indicate tendency towards significance. (): Significance levels in brackets indicate that the respective significance is lost after Bonferroni corrections are applied.

Friedman-Test **FAs-allReg**	**pre-dur-post**		**pre-dur**		**dur-post**		**pre-post**	
	χ^2	***p***	χ^2	***p***	χ^2	***p***	χ^2	***p***
rest	45.704	0.000	39.706	0.000	18.000	0.000	3.314	(*0.065*)
comfort	3.045	0.218	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
breed	2.080	0.353	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
vigilance	56.581	0.000	36.255	0.000	36.255	0.000	3.920	(0.048)
agonistics	2.187	0.335	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
headshakes	10.093	0.006	8.805	0.003	1.089	0.297	4.333	(0.037)
posture: 'prone'	9.950	0.007	8.526	0.004	3.429	(*0.064*)	1.778	0.182

With respect to ***individual regimes***, tables 5.3.2-4 and 5.3.2-5 give a comprehensive overview concerning direction – but not magnitude – of changes in proportions between periods (whereby up = increase, down = decrease, and same = unchanged values). Results on each parameter will be verbalised in the following sections together with magnitudes of difference between ***different visiting regimes***; which have been visualised with the help of boxplots (s.b., parameter-specific subsections).

As for ***individual sessions***, the table in appendix 5.3.2-3.01 shows exact proportions calculated for each session (but can hardly be recommended as healthy reading, and has therefore been 'appendicited'). Response range across individual sessions can be gauged from between-period differences tabulated at the beginning of each parameter-specific subsection (e.g., tab. 5.3.2-6).

Table 5.3.2-4: Overview of Proportional Changes in Behaviour Systems and Headshakes Between Periods. Figures depict number of sessions for all regimes/ each regime for which proportions of behaviour changed in the respective direction. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; Σ: sum of; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y); FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; %: proportion; pre: before visitation, dur: during visitation, post: after visitation; →: from … to; up: increase, down: decrease, same: unchanged values.

direction of change	**%_rest**									**%_comfort**								
	pre → dur			**dur → post**			**pre → post**			**pre → dur**			**dur → post**			**pre → post**		
	up	same	down	up	same	down	up	same	down	up	same	down	up	same	down	up	same	down
Σ FAs-allReg	3	0	48	40	1	10	19	0	32	19	22	10	18	17	16	20	20	11
Σ FAs-B$_1$	1	0	16	14	0	3	6	0	11	3	11	3	8	6	3	8	5	4
Σ FAs-C$_{1,2}$	1	0	15	12	1	3	7	0	9	6	6	4	4	6	6	4	8	4
Σ FAs-X	1	0	11	10	0	2	4	0	8	7	4	1	5	3	4	7	4	1
Σ FAs-Y	0	0	6	4	0	2	2	0	4	3	1	2	1	2	3	1	3	2

direction of change	**%_breed**									**%_vigilance**								
	pre → dur			**dur → post**			**pre → post**			**pre → dur**			**dur → post**			**pre → post**		
	up	same	down	up	same	down	up	same	down	up	same	down	up	same	down	up	same	down
Σ FAs-allReg	27	3	21	26	0	25	28	2	21	47	0	4	4	0	47	32	1	18
Σ FAs-B$_1$	11	1	5	7	0	10	11	2	4	16	0	1	0	0	17	10	0	7
Σ FAs-C$_{1,2}$	7	1	8	10	0	6	7	0	9	13	0	3	2	0	14	8	0	8
Σ FAs-X	5	0	7	6	0	6	6	0	6	12	0	0	1	0	11	8	1	3
Σ FAs-Y	4	1	1	3	0	3	4	0	2	6	0	0	1	0	5	6	0	0

direction of change	**%_agonistics**									**%_headshakes**								
	pre → dur			**dur →post**			**pre → post**			**pre → dur**			**dur → post**			**pre → post**		
	up	same	down	up	same	down	up	same	down	up	same	down	up	same	down	up	same	down
Σ FAs-allReg	28	6	17	20	7	24	24	5	22	30	10	11	19	6	26	26	12	13
Σ FAs-B$_1$	7	3	7	6	4	7	5	3	9	9	7	1	8	3	6	9	7	1
Σ FAs-C$_{1,2}$	12	0	4	7	0	9	10	0	6	10	0	6	5	1	10	8	1	7
Σ FAs-X	5	3	4	4	3	5	6	1	5	6	3	3	4	2	6	6	2	4
Σ FAs-Y	4	0	2	3	0	3	3	1	2	5	0	1	2	0	4	3	2	1

Table 5.3.2-5: Overview of Proportional Changes in Time Spent in Two Mutually Exclusive Postures Between Periods. Figures depict number of sessions for all regimes/ each regime for which proportions of a given posture changed in the respective direction. _prone: lying, _up: sitting/ standing; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y); FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; %: proportion; pre: before visitation, dur: during visitation, post: after visitation; →: from … to; up: increase, down: decrease, same: unchanged values.

direction of change	%_prone									%_up								
	pre → dur			dur → post			pre → post			pre → dur			dur → post			pre → post		
	up	same	down	up	same	down	up	same	down	up	same	down	up	same	down	up	same	down
sum FAs-allReg	10	13	28	27	9	15	14	15	22	28	13	10	15	9	27	22	15	14
sum FAs-B$_1$	2	6	9	7	3	7	1	8	8	9	6	2	7	3	7	8	8	1
sum FAs-C$_{1,2}$	4	3	9	10	3	3	7	3	6	9	3	4	3	3	10	6	3	7
sum FAs-X	3	3	6	6	2	4	4	2	6	6	3	3	4	2	6	6	2	4
sum FAs-Y	1	1	4	4	1	1	2	2	2	4	1	1	1	1	4	2	2	2

5.3.2.1.4 Resting Behaviour

For ***all regimes*** together, proportions of **pre-visit resting behaviour** ranged from 7 % to 97 % (median: 61 %; tab. 5.3.2-6).

At ***individual regimes*** (fig. 5.3.2-1), median proportions of pre-visit resting behaviour were lowest for FAs-$C_{1,2}$ (46 %). They were markedly higher and approximately equal for FAs subjected to the other three regimes (FAs-B_1: 74 %, FAs-X: 75 %, FAs-Y: 76 %).

Table 5.3.2-6: Resting Behaviour – Descriptive Statistics for Periods and Between-Period Differences. For between-period differences, positive values represent increases, negative values represent decreases. **N.b.:** Minimum negative values represent most pronounced decrease, and maximum negative values constitute least pronounced decrease. pre: prior to visitation, during: during visitation, post: after visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y); min.: minimum, Q 1: 1st quartile (25 %), Q 3: 3rd quartile (75 %), max.: maximum. Between-period differences include MoD-values (median of differences); DiM-values (difference in median) are attained by subtracting pre- from dur-, dur- from post-, and pre- from post-visit values, resp.

Comportment Parameter	**Period/ Between-Period Difference**		**FAs-allReg**				
			min.	Q 1	**median**	Q 3	max.
Rest	Period	pre	6.50	36.80	**60.70**	84.80	97.10
		during	1.90	8.90	**21.10**	40.75	70.50
		post	3.70	22.35	**43.80**	71.85	89.70
	Between-Period Difference	pre to during	-83.30	-52.85	**-29.57**	-14.70	9.40
		during to post	-36.50	1.80	**20.40**	42.25	69.20
		pre to post	-92.70	-39.20	**-9.50**	12.50	43.70

Looking at ***all regimes*** together, the proportion of time spent resting differed significantly **among the three periods** (Friedman-test: χ^2=45.704, *p*=0.000; tab. 5.3.2-3): During-visit proportions (median: 21 %) were distinctly smaller than pre-visit proportions (median: 61 %), while post-visit proportions (median: 44 %) were smaller than pre-, but greater than during-visit ones (tab. 5.3.2-6).

Figure 5.3.2-1 shows between-period changes found at ***individual regimes***: While the basic pattern described above (directions of change) is found in all regimes, regime differences become evident. Boxplots visualise the extent of variability and also indicate that pre-visit proportions, as well as the extent of response and recovery were different in ***individual sessions***.

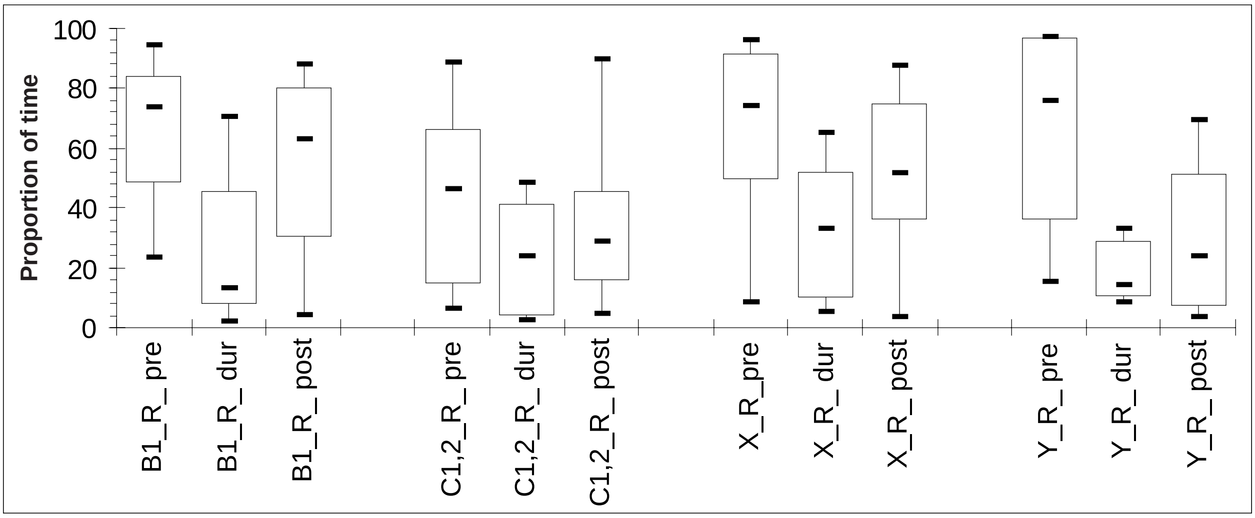

Figure 5.3.2-1: Proportion of Time Spent Resting before, during, and after Human Visitation. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; _R = resting behaviour; pre = pre-visit, dur = during-visit, post = post-visit. Boxplot-values depict minimum, 25 %, median, 75 %, and maximum for each regime.

Comparing the periods **before and during** human visitation, the proportion of resting behaviour calculated for ***all regimes*** together diminished markedly in the latter (DiM = difference in medians: -40 %; tab. 5.3.2-6). Friedman-test indicated a highly significant difference (pre-visit vs. during-visit: χ^2=39.706, *p*=0.000; tab. 5.3.2-3) suggesting that visitor presence and action resulted in a pronounced overall response.

Looking at ***individual regimes*** (appendix 5.3.2-3.05), the difference in medians was highest for FAs-Y and FAs-B_1 (decreases by -62 % and -60 %, resp.), distinctly lower for FAs-X (decrease by -42 %), and least pronounced for FAs-$C_{1,2}$ (decrease by -23 %).

As for ***individual sessions***, resting behaviour decreased (as compared to pre-visit) in 48 sessions, never remained unchanged, and an increase in resting behaviour from before to during visitation was found in 3 sessions only (tab. 5.3.2-4): once each at FAs-B_1 (by +9 %), FAs-$C_{1,2}$ (by +9 %), and FAs-X (by +1 %; appendix 5.3.2-3.01). The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-6) in proportions of resting behaviour between pre- and during- visitation amounted to -30 % (range: -83 % to +9 %).

Pooled by regime (appendix 5.3.2-3.06), response levels per session were most pronounced at FAs-Y, with a MoD-value amounting to -52 % (range: -83 % to -4 %), followed by FAs-X (MoD: -33 %; range: -76 % to +1 %) and FAs-B_1 (MoD: -30 %; range: -77 % to +9 %), and least pronounced at FAs-$C_{1,2}$ (MoD: -23 %; range: -53 % to +9 %).

Between the periods **during and after** human visitation, the difference in proportion of resting behaviour calculated for ***all regimes*** together was likewise highly significant (during-visit vs. post-visit: χ2=18.000, *p*=0.000; tab. 5.3.2-3), with a marked increase (difference in medians: +23 %; tab. 5.3.2-6) found during the latter period. As regards the behaviour system of rest, visitor withdrawal thus resulted in a pronounced overall response, viz., a re-increase in resting behaviour.

With respect to ***individual regimes***, the difference in medians (appendix 5.3.2-3.05) was highest at FAs-B_1 (increase by +50 %), followed by FAs-X (increase by +19 %), FAs-Y (increase by +10 %), and FAs-C (increase by +5 %).

As for ***individual sessions***, post-visit proportions of resting behaviour increased (as compared to during-visit) in 40 sessions. No difference was found in 1 session at FAs-$C_{1,2}$ (during-visit = post-visit = 13.5 %; appendix 5.3.2-3.01). Proportions decreased in 10 sessions (tab. 5.3.2-4). The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-6) in proportions of resting behaviour between during- and post-visitation, amounted to +20 % (range: -37 % to +69 %).

Pooled by regime (appendix 5.3.2-3.06), response levels per session were most pronounced at FAs-B_1, with a median of differences (all sessions per regime) of +34 % (range: -36 % to +69 %), followed by FAs-X (MoD: +23 %; range: -37 % to +64 %) and less pronounced at FAs-$C_{1,2}$ (MoD: +16 %; range: -26 % to +49 %) and FAs-Y (MoD: +14 %; range: -9 % to +36 %), indicating that for the latter two, waning of during-visit response (decreased rest) was not as prominent as for the former.

With respect to the periods **before and after** human visitation, global Friedman-test did not indicate a significant difference between proportions of resting behaviour calculated for ***all regimes*** together (Friedman-test: χ^2=3.314, *p*=0.065; tab. 5.3.2-3), even though median resting levels post-visit were still lower than pre-visit by -17 % (tab. 5.3.2-6).

As regards resting behaviour, overall response suggests that recovery was ‘on the way’ but not completely effected yet.

Looking at ***individual regimes*** (appendix 5.3.2-3.05), median post-visit resting values remained well below those found before human visitation at each of the regimes. The difference in medians was least pronounced at FAs-B_1 (decrease by -11 %), followed by FAs-$C_{1,2}$ and X (decreases by -18 % and -23 %, resp.), and most pronounced at FAs-Y (decrease by -52 %).

As for ***individual sessions*** (tab. 5.3.2-4), post-visit proportions of resting behaviour decreased (as compared to pre-visit) in 32 sessions and increased in 19 sessions. Post-visit proportions equal to pre-visit ones were never observed. In 10 of 32 sessions (appendix 5.3.2-3.01), the post-visit decrease constituted a ‘continuation’, in that during-visit proportions had already been lower than pre-visit proportions. A continuous increase in proportions of resting behaviour was found in 3 of 19 sessions.

In 63 % of all sessions, post-visit proportions of resting behaviour remained lower than pre-visit proportions, while in 37 % they were higher than observed before the visit.

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-6) in proportions of resting behaviour between pre- and post-visitation amounted to -10 % (range: -93 % to +44 %).

Pooled by regime (appendix 5.3.2-3.06), **extent of recovery** found within each session was most pronounced at FAs-$C_{1,2}$, with a median of differences of only -3 % (range: -61 % to +29 %), followed by FAs-B_1 (MoD: -7%; range: -70 % to +44 %) and FAs-X (MoD: -14 %; range: -83 % to +37 %), and least pronounced at FAs-Y (MoD: -37 %; range: -93 % to +12 %).

5.3.2.1.5 Comfort Behaviour

In summary, the dataset and (descriptive) statistics employed did not yield any consistent differences with respect to proportions of time allotted to comfort behaviour before, during, and after human visitation (tab. 5-3-2-3; tab. 5.3.2-4).

Additionally, the following observations on ***individual sessions*** (appendix 5.3.2-3.01) are of interest:

If prior to human visitation comfort behaviour had been **shown** (15 sessions), it was more likely to be reduced or even totally absent (4 and 7 sessions, resp.) during visitation, than to increase (4 sessions) or remain unaffected (0 sessions). In 3 sessions, in which comfort behaviour had constituted a considerable part of the pre-visit behaviour (14%, 28 %, 67 %, resp.), it was severely reduced or absent during visitation and entirely absent post-visitation.

If prior to human visitation comfort behaviour had **not** been **shown** (36 sessions), it was more likely to remain absent (22 sessions) than to be exhibited during visitation (14 sessions).

In conclusion, it is suggested that analysis of a more extensive dataset containing a greater overall proportion of comfort behaviour might result in biologically relevant information as regards the sensitivity of comfort behaviour to human visitation.

For the indefatigable reader, a more detailed account is given below.

For ***all regimes*** together, proportions of **pre-visit comfort behaviour** ranged from 0 % to 67 % (median: 0 %; tab. 5.3.2-7).

Due to general scarcity of occurrence, median proportions of pre-visit comfort behaviour amounted to 0 % at all ***individual regimes*** (fig. 5.3.2-2).

Absence of comfort behaviour throughout the session was found in 13 of 51 sessions: in 5 of 17 sessions at FAs-B_1, 4 of 16 sessions at FAs-$C_{1,2}$, 3 of 12 sessions at FAs-X, and 1 of 6 sessions at FAs-Y (appendix 5.3.2-3.01).

Table 5.3.2-7: Comfort Behaviour – Descriptive Statistics for Periods and Between-Period Differences. For between-period differences, positive values represent increases, negative values represent decreases. **N.b.:** Minimum negative values represent most pronounced decrease, and maximum negative values constitute least pronounced decrease. pre: prior to visitation, during: during visitation, post: after visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y); min.: minimum, Q 1: 1st quartile (25 %), Q 3: 3rd quartile (75 %), max.: maximum. Between-period differences include MoD-values (median of differences); DiM-values (difference in median) are attained by subtracting pre- from dur-, dur- from post-, and pre- from post-visit values, resp.

Comportment Parameter	**Period/ Between-Period Difference**		**FAs-allReg**				
			min.	Q 1	**median**	Q 3	max.
Comfort	Period	pre	0.00	0.00	**0.00**	0.20	66.90
		during	0.00	0.00	**0.00**	0.60	20.10
		post	0.00	0.00	**0.00**	0.55	78.70
	Between-Period Difference	pre to during	-64.50	0.00	**0.00**	0.35	20.10
		during to post	-8.80	-0.20	**0.00**	0.40	74.60
		pre to post	-66.90	0.00	**0.00**	0.45	78.10

Looking at ***all regimes*** together, the proportion of time spent engaged in comfort behaviours did not differ significantly **among the three periods** (Friedman-test: χ^2=3.045, p=0.218; tab. 5.3.2-3). Consequently, no pair-wise Friedman-tests were performed.

With respect to ***individual regimes***, figure 5.3.2-2 shows that changes between periods mainly consisted of varying maxima and 3rd quartile-values. They rarely affected the median and never altered minima or 1st quartile-values.

Comparing the periods **before and during** human visitation for ***individual regimes*** (appendix 5.3.2-3.05), the difference in medians was ‘highest’ at FAs-Y (increase by +0.90 %), distinctly lower at FAs-X and FAs-C (increases by +0.10 %), and absent at FAs-B_1.

As for ***individual sessions*** (tab. 5.3.2-4), an increase in comfort behaviour from **before to during** visitation was found in 19 sessions. Proportions of comfort behaviour remained unchanged in 22 sessions, and decreased in 10 sessions. Changes in either direction were least common at FAs-B_1 (11 of 17 sessions unchanged). At FAs-$C_{1,2}$, increases were more often observed than decreases (but equally often as no changes), and at FAs-X and FAs-Y, increases were noted in at least half of all visiting sessions.

The median of differences across all sessions of all regimes (magnitude of within-session response; tab. 5.3.2-7) in proportions of comfort behaviour between pre- and during-visitation amounted to zero (MoD: 0 %; range: -65 % to +20 %), even though range indicated that individual responses in either direction had been quite distinct.

Medians of differences across all sessions per regime (appendix 5.3.2-3.06) were negligible and only found at FAs-Y (MoD: +0.30 %; range: -65 % to +20 %) and FAs-X (MoD: +0.10 %; range: -9 % to +9 %). At FAs-B_1 (range: -5 % to +0.50%) and $C_{1,2}$ (range: -28 % to +7 %), MoD-values amounted to 0 %, even though range-values for the latter indicated that individual responses, particularly decreases, had been quite distinct.

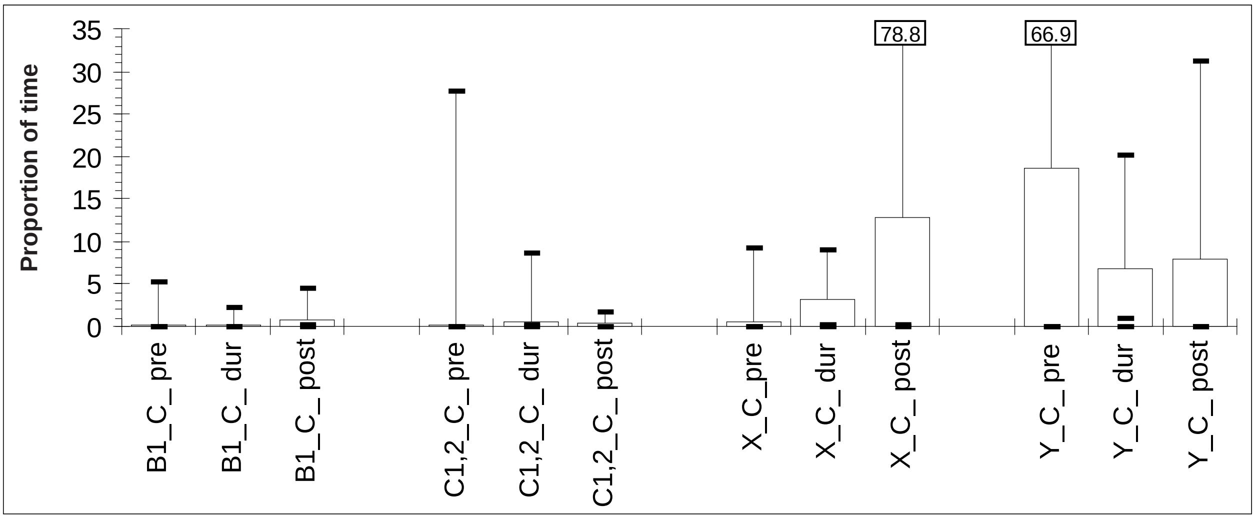

Figure 5.3.2-2: Proportion of Time Spent Performing Comfort Behaviours before, during, and after Human Visitation. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; _C = comfort behaviour; pre = pre-visit, dur = during-visit, post = post-visit. Boxplot-values depict minimum, 25 %, median, 75 %, and maximum for each regime.

During and after human visitation, the difference in proportion of comfort behaviour between the periods remained slight with respect to ***individual regimes*** (appendix 5.3.2-3.05). Proportions of comfort behaviour decreased at FAs-$C_{1,2}$ and FAs-Y, and increased at FAs-B_1 and FAs-X. The difference in medians was 'highest' at FAs-Y (decrease by -0.90 %), followed by FAs-X (further increase by +0.15 %), and negligible at FAs-B_1 and FAs-$C_{1,2}$ (FAs-B_1: increase by +0.10 %; FAs-$C_{1,2}$: decrease by -0.10 %).

As for ***individual sessions***, post-visit proportions of comfort behaviour increased as compared to during-visit in 18 sessions. They remained unchanged in 17 sessions, and decreased in 16 sessions (tab. 5.3.2-4).

The median of differences across all sessions of all regimes (magnitude of within-session response; tab. 5.3.2-7) in proportions of comfort behaviour between during- and post-visitation amounted to zero (MoD: 0 %; range: -9 % to +75 %).

A negligible median of differences per regime was only found at FAs-Y (MoD: -0.30 %; range: -2 % to +11 %). At FAs-B_1 (range: -2 % to +4%), FAs-$C_{1,2}$ (range: -9 % to +0.80 %), and FAs-X (range: -9 % to +75 %), MoD-values amounted to 0 %. In the latter, range indicated that individual responses in the form of increased comfort behaviour had been obtained (appendix 5.3.2-3.06).

Before and after human visitation at ***individual regimes*** (appendix 5.3.2-3.05), there was no difference in medians between proportions of comfort behaviour for the periods for FAs-$C_{1,2}$ and FAs-Y, and a negligible increase at FAs-B_1 (by 0.10 %). At FAs-X (continued increase), the difference amounted to +0.25 %.

As for ***individual sessions***, post-visit proportions of comfort behaviour increased (as compared to pre-visit) in 20 sessions. They remained unchanged in another 20 sessions, and decreased in 11 sessions (tab. 5.3.2-4). A continuous increase was found in 6 sessions (all of which had pre-visit proportions <1 %), while a continuous decrease occurred in 4 sessions. In one of these sessions, the pre-visit proportion had been substantial (67 %), in 1 session it was above 10 % (14 %), whereas the proportion was below 5 % (4 %) in the third, and below 1 % (0.3 %) in the last session (appendix 5.3.2-3.01).

In 39 % of all sessions, post-visit proportions of comfort behaviour remained higher than pre-visit proportions, while in 22 %, they were lower than observed prior to visitation.

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-7) in proportions of comfort behaviour between pre- and post-visitation amounted to zero (MoD: 0 %; range: -67 % to +78 %).

A negligible median of differences per regime was only found at FAs-X (MoD: +0.15 %; range: -0.20 % to +78 %). At FAs-B_1 (range: -4 % to +5%), FAs-$C_{1,2}$ (range: -28 % to +2 %), and FAs-Y (range: -67 % to +31 %), MoD-values amounted to 0 %. For the latter two, ranges indicated that individual responses in either direction (FAs-Y), respectively decreases (FAs-$C_{1,2}$) had been quite distinct (appendix 5.3.2-3.06).

5.3.2.1.6 Breeding Behaviour

In summary, the dataset and (descriptive) statistics employed did not yield any consistent differences with respect to proportions of time allotted to breeding behaviour before, during, and after human visitation (tab. 5.3.2-3; tab. 5.3.2-4).

Additionally, the following observations on ***individual sessions*** (appendix 5.3.2-3.01) are of interest:

If prior to human visitation breeding behaviour had constituted a **considerable proportion** (= 10 %) of all behaviours (6 sessions), it invariably decreased during visitation. Pre-visit proportions of breeding behaviour between 5 % and 10 % were likewise found to decrease in 6 out of 7 sessions. In contrast, pre-visit proportions between 1 % and 5 % were equally likely to increase as to decrease/ remain unchanged (7 vs. 7 sessions).

If prior to human visitation breeding behaviour had **not** been **shown** (14 sessions), it was far more likely to be exhibited (12 sessions) than to remain absent during visitation (2 sessions).

In conclusion, it is suggested that analysis of a more extensive dataset containing a greater overall proportion of breeding behaviour might result in biologically relevant information as regards the sensitivity of breeding behaviour to human visitation.

For the indefatigable reader, a more detailed account is given below.

For ***all regimes*** together, proportions of **pre-visit breeding behaviour** ranged from 0 % to 20 % (median: 1.10 %; tab. 5.3.2-8).

At ***individual regimes*** (fig. 5.3.2-3), median proportions of pre-visit breeding behaviour were lowest at FAs-B_1 (0 %). They were very slightly higher at FAs-Y (0.55 %), and 'highest' at FAs-$C_{1,2}$ and X (3 %).

The proportion of time spent performing breeding behaviours did not differ significantly **among the three periods** (global Friedman-test: χ^2= 2.080, p=0.353; tab. 5.3.2-3). Consequently, no pair-wise tests were performed.

With respect to ***individual regimes***, figure 5.3.2-3 shows that changes between periods mainly consisted of varying maxima and 3rd quartile-values, while – with the exception of FAs-Y – median-values were far less affected.

Table 5.3.2-8: Breeding Behaviour – Descriptive Statistics for Periods and Between-Period Differences. For between-period differences, positive values represent increases, negative values represent decreases. **N.b.:** Minimum negative values represent most pronounced decrease, and maximum negative values constitute least pronounced decrease. pre: prior to visitation, during: during visitation, post: after visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y); min.: minimum, Q 1: 1st quartile (25 %), Q 3: 3rd quartile (75 %), max.: maximum. Between-period differences include MoD-values (median of differences); DiM-values (difference in median) are attained by subtracting pre- from dur-, dur- from post-, and pre- from post-visit values, resp.

Comportment Parameter	**Period/ Between-Period Difference**		**FAs-allReg**				
			min.	Q 1	**median**	Q 3	max.
Breed	Period	pre	0.00	0.00	**1.10**	4.82	19.80
		during	0.00	0.70	**2.50**	6.30	17.50
		post	0.00	0.90	**2.10**	13.10	56.90
	Between-Period Difference	pre to during	-17.40	-2.95	**0.24**	4.30	17.10
		during to post	-15.20	-2.15	**0.20**	7.30	41.10
		pre to post	-17.70	-2.57	**0.60**	6.00	56.50

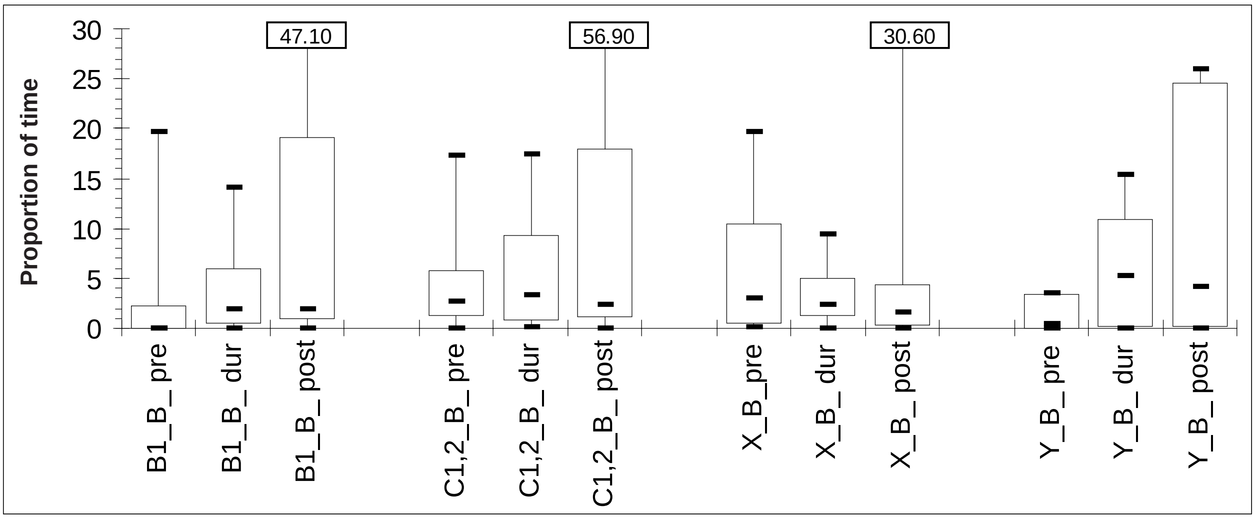

Figure 5.3.2-3: Proportion of Time Spent Performing Breeding Behaviours before, during, and after Human Visitation. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; _B = breeding behaviour; pre = pre-visit, dur = during-visit, post = post-visit. Boxplot-values depict minimum, 25 %, median, 75 %, and maximum for each regime. Numbers/ figures in text fields represent values for cut-off maxima.

Comparing the periods **before and during** human visitation for ***individual regimes*** (appendix 5.3.2-3.05), the proportion of breeding behaviour decreased slightly at FAs-X, and increased at the other regimes: The difference in medians was ‘highest’ at FAs-Y (increase by +5 %), followed by FAs-B_1 (increase by +2 %), and negligible for FAs-$C_{1,2}$ (increase by +0.55 %) and FAs-X (decrease by -0.60 %).

As for ***individual sessions*** (tab. 5.3.2-4), an increase in breeding behaviour from **before to during** visitation was found in 27 sessions. Proportions of breeding behaviour remained unchanged in 3 sessions, and decreased in 21 sessions. Increases were more common than decreases in FAs-B_1 (11 of 17 sessions) and FAs-Y (4 of 6 sessions), where proportions of pre-visit breeding behaviour had been very low. At FAs-$C_{1,2}$ and FAs-X (medians pre-visit: 3 %), increases roughly equalled decreases (7 vs. 8 sessions, and 5 vs. 7 sessions, resp.).

The median of differences (MoD; magnitude of within-session response across all sessions; tab. 5.3.2-8) in proportions of breeding behaviour between pre- and during-visitation amounted to only +0.24 % (range: -17 % to +17 %).

Direction of response per session differed among regimes (appendix 5.3.2-3.06), with positive MoD-values found at FAs-Y (+5 %; range: -3 % to +12 %) and FAs-B_1 (MoD: +0.70 %; range: -6 % to +13 %), while MoD-values were negative at FAs-X (-2 %; range: -17 % to +9 %) and FAs-$C_{1,2}$ (-0.15 %; range: -16 % to +17 %).

Between the periods **during and after** human visitation, the difference in proportion of breeding behaviour was very slight (difference in medians = 1 %) with respect to ***individual regimes*** (appendix 5.3.2-3.05): Proportions of breeding behaviour decreased at FAs-$C_{1,2}$ (by -0.95 %), FAs-X (by -0.75 %) and FAs-Y (by -1 %), and negligibly increased at FAs-B_1 (by +0.10 %).

As for ***individual sessions*** (tab. 5.3.2-4), post-visit proportions of breeding behaviour increased (as compared to during-visit) in 26 sessions, never remained unchanged, and decreased in 25 sessions. At FAs-B_1, increases were less common than decreases (7 vs. 10 sessions). At FAs-$C_{1,2}$, the reverse was true (increase in 10 sessions vs. decrease in 6 sessions). At FAs-X (6 vs. 6) and FAs-Y (3 vs. 3), increases equalled decreases.

The median of differences (MoD; magnitude of within-session response across all sessions; tab. 5.3.2-8) in proportions of breeding behaviour between during- and post-visitation amounted to only +0.20 % (range: -15 % to +41 %).

Direction of response per session differed among regimes, with positive MoD-values found at FAs-Y (+3 %; range: -15 % to 18 %) and FAs-$C_{1,2}$ (MoD: +0.45 %; range: -8 % to +39 %). MoD-values were negative and next to negligible at FAs-B_1 (-0.24 %; range: -12 % to +41 %) and FAs-X (continuing decrease, MoD: -0.05 %; range: -8 % to +28 %), even though range indicated that individual responses in either direction, and particularly increases in breeding behaviour, had been quite distinct.

For the periods **before and after** human visitation at ***individual regimes*** (appendix 5.3.2-3.05), the difference in medians between proportions of breeding behaviour was ‘highest’ for FAs-Y (increase by +4 %), followed by FAs-B_1 (increase by +2 %). FAs-$C_{1,2}$ and FAs-X showed negligibly or slightly decreased breeding behaviour as compared to pre-visit (by -0.40 % and -1 %, resp.).

As for ***individual sessions*** (tab. 5.3.2-4), post-visit proportions of breeding behaviour increased (as compared to pre-visit) in 28 sessions. They remained unchanged in 2 sessions, and decreased in 21 sessions. At FAs-B_1 and Y, increases were (far) more common than decreases (11 vs. 4 sessions, and 4 vs. 2 sessions, resp.), while increases (roughly) equalled decreases at FAs-$C_{1,2}$ and X (7 vs. 9 sessions, and 6 vs. 6 sessions, resp.). A continuous increase was found in 13 sessions, for only two of which pre-visit proportions had exceeded 1 % (appendix 5.3.2-3.01). A continuous decrease (appendix 5.3.2-3.01) occurred in 8 sessions. Of these, pre-visit proportions had exceeded 10 % (max.: 20 %) in 3 sessions, in 4 sessions, proportions ranged between 5 % and <10 % (max.: 9.9 %), and in only 1 session, pre-visit proportions had been lower than 5 % (4 %).

In 55 % of all sessions, post-visit proportions of breeding behaviour remained higher than pre-visit proportions, while in 41 %, they were lower than observed prior to visitation.

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-8) in proportions of breeding behaviour between pre- and post-visitation amounted to only +0.60 % (range: -18 % to +57 %).

With respect to **recovery**, MoD-values for breeding behaviour pooled by regime were slightly higher at FAs-Y (+4 %; range: -4 % to +26 %) and FAs-B_1 (MoD: +2 %; range: -18 % to +39 %). At

FAs-$C_{1,2}$ (MoD: -0.70 %; range -17 % to +57%), and FAs-X (MoD: +0.20 %; range: -16 % to +30 %), there was approximately no change in MoD-value, even though range indicated that individual responses in either direction, but particularly increases in breeding behaviour, had been quite distinct.

5.3.2.1.7 Vigilance Behaviour

For ***all regimes*** together, proportions of **pre-visit vigilance behaviour** ranged from 2 % to 82 % (median: 28 %; tab. 5.3.2-9).

Table 5.3.2-9: Vigilance Behaviour – Descriptive Statistics for Periods and Between-Period Differences. For between-period differences, positive values represent increases, negative values represent decreases. **N.b.:** Minimum negative values represent most pronounced decrease, and maximum negative values constitute least pronounced decrease. pre: prior to visitation, during: during visitation, post: after visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y); min.: minimum, Q 1: 1st quartile (25 %), Q 3: 3rd quartile (75 %), max.: maximum. Between-period differences include MoD-values (median of differences); DiM-values (difference in median) are attained by subtracting pre- from dur-, dur- from post-, and pre- from post-visit values, resp.

Comportment Parameter	**Period/ Between-Period Difference**		**FAs-allReg**				
			min.	Q 1	**median**	Q 3	max.
Vigilance	Period	pre	1.90	12.10	**27.60**	47.45	82.10
		during	28.20	51.50	**63.80**	78.50	97.50
		post	5.10	20.30	**33.90**	54.00	78.90
	Between-Period Difference	pre to during	-11.00	17.30	**32.40**	47.35	72.90
		during to post	-64.60	-37.55	**-30.70**	-16.70	17.60
		pre to post	-35.20	-12.95	**8.30**	16.20	57.30

At ***individual regimes*** (fig. 5.3.2-4), median proportions of pre-visit vigilance behaviour were lowest at FAs-X and FAs-Y (13 % and 16 %, resp.), followed by FAs-B_1 (26 %), and highest at FAs-$C_{1,2}$ (41 %).

Looking at ***all regimes*** together, the proportion of vigilance differed significantly **among the three periods** (global Friedman-test: χ^2=56.581, *p*=0.000; tab. 5.3.2-3): During-visit proportions (64 %) were distinctly greater than pre-visit proportions (28 %), while post-visit proportions (34 %) were slightly greater than pre-, but smaller than during-visit ones (tab. 5.3.2-9).

Figure 5.3.2-4 shows changes between periods found at ***individual regimes***: While the basic pattern described above (directions of change) is found in all regimes, regime differences become evident. Boxplots visualise the extent of variability and also indicate that pre-visit proportions, as well as the extent of response and recovery were different in ***individual sessions***.

Comparing the periods **before and during** human visitation for ***all regimes***, the proportion of vigilance behaviour increased markedly in the latter (difference in medians, DiM: +36 %; tab. 5.3.2-9). Pair-wise Friedman-test indicated a highly significant difference (pre-visit vs. during-visit: χ^2=36.255, *p*=0.000; tab. 5.3.2-3) suggesting that visitor presence and action resulted in a pronounced overall response.

Looking at ***individual regimes*** (appendix 5.3.2-3.05), the difference in medians was highest at FAs-Y (increase by +51 %), followed by FAs-X and FAs-B (increases by +45 % and +40 %, resp.), and least pronounced at FAs-$C_{1,2}$ (increase by +23 %). This resulted in a range of during-visit medians (58 % to 67 %) far narrower than prior to visitation (13 % to 41 %, s.a.).

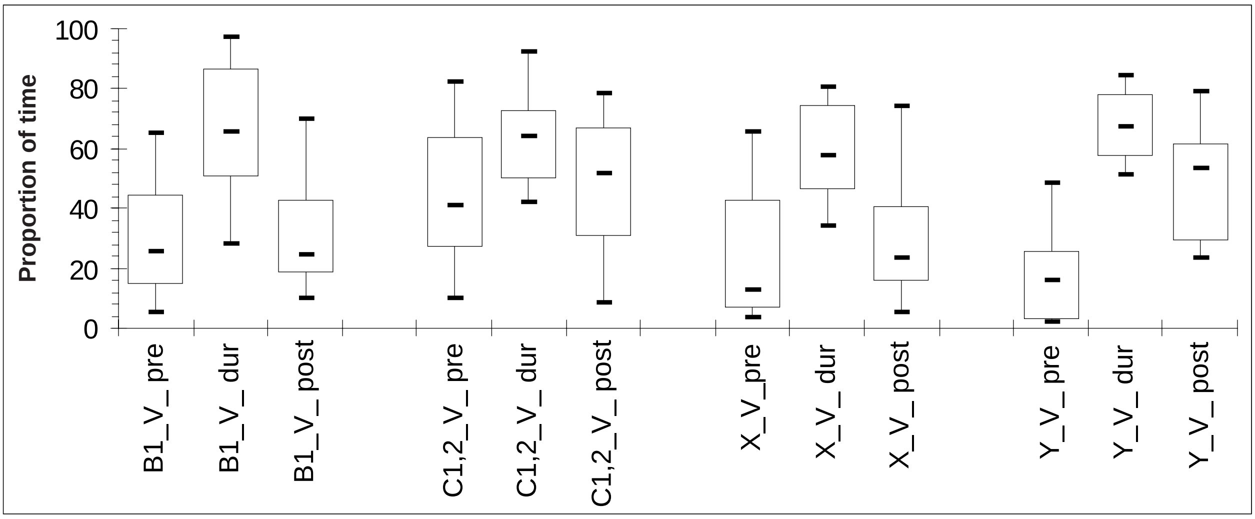

Figure 5.3.2-4: Proportion of Time Spent Vigilant before, during, and after Human Visitation. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; _V = vigilance behaviour; pre = pre-visit, dur = during-visit, post = post-visit. Boxplot-values depict minimum, 25 %, median, 75 %, and maximum for each regime.

As for ***individual sessions***, a decrease in vigilance behaviour from before to during visitation was found in 4 sessions only (tab. 5.3.2-4); once at FAs-B_1 (by -3 %), and three times at FAs-$C_{1,2}$ (by -11 %, -1 %, and -0.8 %, resp.; appendix 5.3.2-3.01). Proportions never remained unchanged and increased in 47 sessions (tab. 5.3.2-4).

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-9) in proportions of vigilance behaviour between pre- and during-visitation, amounted to +32 % (range: -11 % to +73 %).

Pooled by regime (appendix 5.3.2-3.06), response levels per session were most pronounced at FAs-Y, with a median of differences of +52 % (range: +22 % to +72 %), followed by FAs-B_1 (MoD: +42 %; range: -3 % to +73 %) and FAs-X (MoD: +35 %; range: +12 % to +50 %), and least pronounced at FAs-$C_{1,2}$ (MoD: +23 %; range: -11 % to +43 %).

Between the periods **during and after** human visitation, the difference in proportion of vigilance behaviour was likewise highly significant (tab. 5.3.2-3: during-visit vs. post-visit: χ^2=36.255, p=0.000), with marked decreases (difference in medians: -30 %; tab. 5.3.2-9) found during the latter period in ***all regimes***. As regards the behaviour system of vigilance, visitor withdrawal thus resulted in a pronounced reduction of overall response.

With respect to ***individual regimes*** (appendix 5.3.2-3.05), the difference in medians was highest at FAs-B_1 (decrease by -41 %), followed by FAs-X (decrease by -34 %), and much lower at FAs-Y and FAs-$C_{1,2}$ (decreases by -14 % and -12 %, resp.).

As for ***individual sessions***, post-visit proportions of vigilance behaviour increased (as compared to during-visit) in 4 sessions only, for one of which during-visit proportion had been lower than the pre-visit one (appendix 5.3.2-3.01). Proportions never remained unchanged and decreased in 47 sessions (tab. 5.3.2-4).

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-9) in proportions of vigilance behaviour between during- and post-visitation amounted to -31 % (range: -65 % to +18 %).

Pooled by regime (appendix 5.3.2-3.06), response levels per session were most pronounced at FAs-B$_1$, with a <u>median of differences</u> of -38 %, and an entirely negative range (-65 % to -9%), i.e. vigilance decreased in all sessions observed. MoD-values were slightly lower at FAs-X (-33%; range, -45 % to +2 %), and less pronounced at FAs-C$_{1,2}$ (MoD: -21 %; range: -39 % to +18 %) and FAs-Y (MoD: -20 %; range: -36 % to +8 %), indicating that for the latter two, waning of during-visit response (increased vigilance) was not as prominent as for the former.

As regards the periods **before and after** human visitation, pair-wise Friedman-test indicated a 'weakly'[1] significant difference between proportions of vigilance behaviour (χ^2=3.920, p=0.048; tab. 5.3.2-3) for ***all regimes***, with difference in medians amounting to just +6 % (tab. 5.3.2-9). As regards vigilance behaviour, overall response suggests that recovery was more or less effected.

Looking at ***individual regimes*** (appendix 5.3.2-3.05), <u>median post-visit</u> vigilance values remained well above those found before human visitation for FAs-C$_{1,2}$, FAs-X, and FAs-Y, but were approximately equal at FAs-B$_1$, resulting in the least pronounced <u>difference in medians</u> at that regime (decrease by -0.80 %). Increases were most pronounced at FAs-Y (by +37 %), and considerably lower at FAs-C$_{1,2}$ and FAs-X (increases by +11 %), indicating a prolonged failure to recover for FAs-Y.

As for ***individual sessions*** (tab. 5.3.2-4), post-visit proportions of vigilance behaviour increased (as compared to pre-visit) in 32 sessions, remained unchanged in 1 session, and decreased in 18 sessions. A <u>continuous increase</u> (with post-visit proportions additionally being higher than during-visit ones) was found in only 3 of 32 sessions. In 3 of 18 sessions, the post-visit <u>decrease</u> constituted a <u>'continuation'</u>, in that during-visit proportions had already been lower than pre-visit proportions (appendix 5.3.2-3.01). With the exception of FAs-C$_{1,2}$ (8 vs. 8 sessions), increases were more common than decreases (tab. 5.3.2-4).

In 63 % of all sessions, post-visit proportions of vigilance behaviour remained higher than pre-visit proportions, while in 35 %, they were lower than observed prior to visitation (tab. 5.3.2-4).

The <u>median of differences</u> (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-9) between pre- and post-visitation for proportions of vigilance behaviour amounted to +8 % (range: -35 % to +57 %).

Pooled by regime (appendix 5.3.2-3.06), **extent of recovery** found within each session was most pronounced at FAs-C$_{1,2}$ and FAs-B$_1$, with <u>MoD</u>-values of only +3 % (range: -33 % to +57 %) and +4 % (range: -35 % to +54 %), respectively. Recovery was less pronounced at FAs-X (MoD: +9 %; range: -21 % to +27 %). It was least pronounced at FAs-Y, with a MoD-value of +34 %, and an exclusively positive range (+6 % to +52 %), i.e., vigilance invariably remained higher than pre-visit.

5.3.2.1.8 Agonistic Behaviour

In summary, the dataset and (descriptive) statistics employed did not yield any consistent differences with respect to proportions of time allotted to agonistic behaviour before, during, and after human visitation (tab. 5.3.2-3; tab. 5.3.2-4).

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[1] i.e., the significance does not survive sequential Bonferroni corrections

Additionally, the following observations on ***individual sessions*** (appendix 5.3.2-3.01) are of interest:

If prior to human visitation agonistic behaviour had been **shown** (34 sessions), it was far more likely to be also shown during visitation (25 sessions) than to be absent (9 sessions); and pre-visit proportions of agonistic behaviour between 5 % and 11 % (6 sessions) invariably resulted in agonistic behaviour forming part of the behavioural repertoire during visitation. During-visit proportions above 5 % (13 sessions) resulted in a post-visit decrease in 11 sessions, while a slight increase (less than 1 %) was found between these periods in the remaining 2 sessions.

If prior to human visitation agonistic behaviour had **not** been **shown** (17 sessions), it was more likely to be exhibited (11 sessions) than to remain absent during visitation (6 sessions).

In conclusion, it is suggested that analysis of a more extensive dataset containing a greater overall proportion of agonistic behaviour might result in biologically relevant information as regards the sensitivity of agonistic behaviour to human visitation.

For the indefatigable reader, a more detailed account is given below.

For ***all regimes*** together, proportions of **pre-visit agonistic behaviour** ranged from 0 % to 11 % (median: 0.90 %; tab. 5.3.2-10). In 28 sessions, pre-visit proportions of agonistic behaviour represented = 1% of all behaviours shown (appendix 5.3.2-3.01).

At ***individual regimes*** (fig. 5.3.2-5), median proportions of pre-visit agonistic behaviour were lowest at FAs-Y (0.45 %). They were slightly higher at FAs-B$_1$ and X (0.70 % and 0.75 %, resp.), and ‘highest’ at FAs-C$_{1,2}$ (2 %).

Looking at ***all regimes*** together, the proportion of time spent performing agonistic behaviours did not differ significantly **among the three periods** (Friedman-test: χ^2=2.187, *p*=0.335; tab. 5.3.2-3). Consequently, no pair-wise tests were performed.

With respect to ***individual regimes***, figure 5.3.2-5 shows that changes between periods mainly consisted of varying maxima and 3rd quartile-values at FAs-B$_1$ and FAs-C$_{1,2}$, while at FAs-X and FAs-Y median-values were affected as well.

Table 5.3.2-10: Agonistic Behaviour – Descriptive Statistics for Periods and Between-Period Differences. For between-period differences, positive values represent increases, negative values represent decreases. **N.b.:** Minimum negative values represent most pronounced decrease, and maximum negative values constitute least pronounced decrease. pre: prior to visitation, during: during visitation, post: after visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y); min.: minimum, Q 1: 1st quartile (25 %), Q 3: 3rd quartile (75 %), max.: maximum. Between-period differences include MoD-values (median of differences); DiM-values (difference in median) are attained by subtracting pre- from dur-, dur- from post-, and pre- from post-visit values, resp.

Comportment Parameter	**Period/ Between-Period Difference**		**FAs-allReg**				
			min.	Q 1	**median**	Q 3	max.
Agonistics	Period	pre	0.00	0.00	**0.90**	3.00	10.60
		during	0.00	0.00	**1.50**	4.90	23.30
		post	0.00	0.15	**1.10**	4.65	14.70
	Between-Period Difference	pre to during	-4.70	-0.52	**0.30**	2.30	18.70
		during to post	-16.90	-2.00	**0.00**	0.55	11.10
		pre to post	-5.40	0.80	**0.00**	1.45	14.70

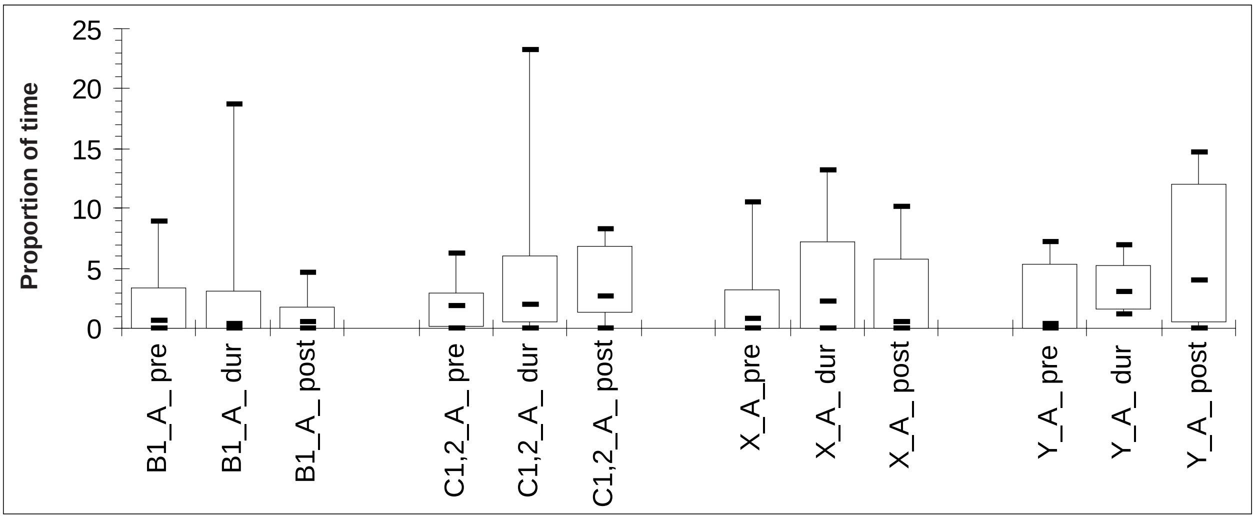

Figure 5.3.2-5: Proportion of Time Spent Performing Agonistic Behaviours before, during, and after Human Visitation. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; _A = agonistic behaviour; pre = pre-visit, dur = during-visit, post = post-visit. Boxplot-values depict minimum, 25 %, median, 75 %, and maximum for each regime.

Comparing the periods **before and during** human visitation for ***individual regimes*** (appendix 5.3.2-3.05), the proportion of agonistic behaviour decreased slightly at FAs-B_1, and increased (slightly) at the other regimes. The difference in medians was 'highest' at FAs-Y (increase by +3 %), followed by FAs-X (increase by +2 %), and negligible for FAs-B_1 (decrease by -0.30 %) and FAs-C (increase by +0.10 %).

As for ***individual sessions***, an increase in agonistic behaviour from before to during visitation was found in 28 sessions. Proportions of agonistic behaviour remained unchanged in 6 sessions, and decreased in 17 sessions (tab. 5.3.2-4). Increases were more common than decreases in FAs-$C_{1,2}$ (12 of 16 sessions) and FAs-Y (4 of 6 sessions), where proportions of pre-visit agonistic behaviour had been particularly low. At FAs-B_1 increases equalled decreases (7 vs. 7 sessions), while at FAs-X, increases, decreases and no change were found in 5, 4, and 3 sessions, respectively.

The median of differences (MoD; magnitude of within-session response across all sessions and regimes; tab. 5.3.2-10) in proportions of agonistic behaviour between pre- and during-visitation amounted to only +0.30 % (range: -5 % to +19 %).

Pooled by regime (appendix 5.3.2-3.06), response levels per session increased at FAs-$C_{1,2}$ (range: -4 % to +17 %) and FAs-Y (range: -0.30 % to +4 %), with median of differences of +1 % each. For FAs-B_1 (range: -5 % to +19 %) and FAs-X (range: -5 % to +13 %), MoD-value was 0 %, even though ranges indicated that individual responses, particularly increases, had been quite distinct.

Comparing the periods **during and after** human visitation with respect to ***individual regimes*** (appendix 5.3.2-3.05), the difference in proportion of agonistic behaviour was negligible to very slight for FAs-B_1, FAs-$C_{1,2}$, and FAs-Y (difference in medians = 1 %; increases by +0.10 %, +0.65 % and +1 %, resp.), and only marginally more pronounced at FAs-X (decrease by -2 %). Proportions of post-visit agonistic behaviour thus increased (as compared to during-visit) at FAs-B_1, FAs-$C_{1,2}$, and FAs-Y, and decreased at FAs-X.

As for ***individual sessions***, post-visit proportions of agonistic behaviour increased (as compared to during-visit) in 20 sessions. They did not change in 7 sessions, and decreased in 24 sessions (tab. 5.3.2-4). For FAs from all 4 regimes, increases approximately equalled decreases.

The median of differences (MoD; magnitude of within-session response across all sessions and regimes; tab. 5.3.2-10) in proportions of agonistic behaviour between during- and post-visitation amounted to zero (MoD: 0 %; range: -17 % to +11 %).

Medians of differences in individual regimes (appendix 5.3.2-3.06) were negative at FAs-$C_{1,2}$ (MoD: -0.75 %; range: -16 % to +8 %) and FAs-Y (MoD: -0.30 %; range: -4 % to +11 %), respectively. For FAs-B_1 (range: -17 % to +4 %) and FAs-X (range: -13 % to +10 %), the median of differences amounted to zero.

For the periods **before and after** human visitation at ***individual regimes*** (appendix 5.3.2-3.05), the difference in medians between proportions of agonistic behaviour was ‘highest’ for FAs-Y (increase by +4 %), and < 1 % for FAs subjected to the other 3 regimes. FAs-B_1 and FAs-X showed marginally decreased agonistic behaviour as compared to pre-visit (by -0.20 % and -0.25 %, resp.), while median proportions showed a negligible increase at FAs-$C_{1,2}$ (+0.75 %).

As for ***individual sessions***, post-visit proportions of agonistic behaviour increased (as compared to pre-visit) in 24 sessions. They remained unchanged in 5 sessions, and decreased in 22 sessions (tab. 5.3.2-4). At FAs-$C_{1,2}$, increases were more common than decreases (10 vs. 6 sessions). The reverse was true for FAs-B_1 (5 vs. 9 sessions), while increases (roughly) equalled decreases at FAs-X and FAs-Y (6 vs. 5 sessions, and 3 vs. 2 sessions, resp.). A continuous increase was found in 7 sessions, for only one of which agonistic behaviour had been observed pre-visitation (2 %; all others: pre-visit proportions = 0.00 %). A continuous decrease occurred in 3 sessions for which pre-visit proportions had amounted to 6 %, 5 %, and 3 %, respectively (appendix 5.3.2-3.01).

In 47 % of all sessions, post-visit proportions of agonistic behaviour remained higher than pre-visit proportions, while in 43 %, they were lower than observed prior to visitation.

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-10) in proportions of agonistic behaviour between pre- and post-visitation amounted to zero (MoD: 0 %; range: -5 % to +15 %).

Pooled by regime (appendix 5.3.2-3.06), **extent of recovery** found within each session was ‘least pronounced’ at FAs-$C_{1,2}$, with a median of differences of +1 % (range: -5 % to +7 %). Negligible median of differences were found at FAs-B_1 (MoD: -0.25 %; range: -4 % to +3 %), and FAs-X (MoD: +0.10 %; range: -5 % to +10 %) and FAs-Y (MoD: +0.10 %; range: -4 % to +15 %).

5.3.2.1.9 Headshakes

N.b.: The reader is reminded that headshake events are extremely short in duration (max.: 3 s). In consequence, the change in proportions, rather than their magnitude ought to be focussed upon.

For ***all regimes*** together, proportions of **pre-visit headshakes** ranged from 0 % to 5 % (median: 0 %; tab. 5.3.2-11).

At ***individual regimes*** (fig. 5.3.2-6), median proportions of pre-visit headshakes equalled 0 % at FAs-B_1 and FAs-Y, followed by FAs-X (0.15 %), and ‘highest’ at FAs-$C_{1,2}$ (0.35 %).

Looking at ***all regimes*** together, the proportion of headshakes differed significantly **among the three periods** (global Friedman-test: χ^2=10.093, *p*=0.006; tab. 5.3.2-3): During-visit proportions (0.4%) were greater than pre-visit proportions (0.0 %), while post-visit proportions (0.2 %) were slightly greater than pre-, but smaller than during-visit ones (tab. 5.3.2-11).

Table 5.3.2-11: Time Spent Performing Headshakes – Descriptive Statistics for Periods and Between-Period Differences. For between-period differences, positive values represent increases, negative values represent decreases. **N.b.:** Minimum negative values represent most pronounced decrease, and maximum negative values constitute least pronounced decrease. pre: prior to visitation, during: during visitation, post: after visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y); min.: minimum, Q 1: 1st quartile (25 %), Q 3: 3rd quartile (75 %), max.: maximum. Between-period differences include MoD-values (median of differences); DiM-values (difference in median) are attained by subtracting pre- from dur-, dur- from post-, and pre- from post-visit values, resp.

Comportment Parameter	**Period/ Between-Period Difference**		**FAs-allReg**				
			min.	Q 1	**median**	Q 3	max.
Headshakes	Period	pre	0.00	0.00	**0.00**	0.35	5.10
		during	0.00	0.00	**0.40**	0.95	3.40
		post	0.00	0.00	**0.20**	0.90	2.80
	Between-Period Difference	pre to during	-4.00	0.00	**0.20**	0.65	3.00
		during to post	-2.60	-0.45	**-0.06**	0.30	2.80
		pre to post	-2.90	-0.10	**0.10**	0.70	2.70

Figure 5.3.2-6 shows changes between periods found at ***individual regimes***: The basic pattern described above (directions of change) is found in all regimes except with respect to FAs-X (continuous increase). Boxplots visualise the extent of variability and also indicate that pre-visit proportions, as well as the extent of response and recovery were different in ***individual sessions***.

Comparing the periods **before and during** human visitation, the proportion of headshakes increased (difference in medians: +0.40 %; tab. 5.3.2-11) in the latter period for ***all regimes***. Pair-wise Friedman-test indicated a significant difference (pre-visit vs. during-visit: χ^2=8.805, *p*=0.003; tab. 5.3.2-3) suggesting that visitor presence and action resulted in a distinct overall response.

Looking at ***individual regimes*** (appendix 5.3.2-3.05), the difference in medians was 'highest' at FAs-Y (increase by +0.55 %), followed by FAs-$C_{1,2}$ and FAs-B_1 (increases by +0.30 % and +0.20 %, resp.), and least pronounced at FAs-X (increase by +0.05 %).

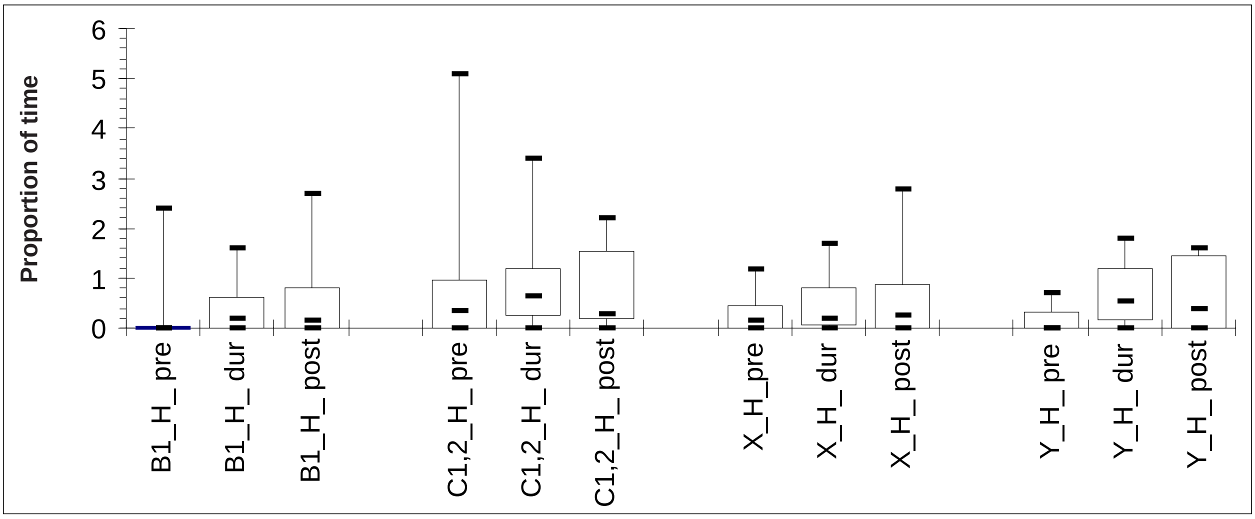

Figure 5.3.2-6: Proportion of Time Spent Performing Headshakes before, during, and after Human Visitation. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; _H = headshakes; pre = pre-visit, dur = during-visit, post = post-visit. Boxplot-values depict minimum, 25 %, median, 75 %, and maximum for each regime.

As for ***individual sessions***, an increase in headshakes from before to during visitation was found in 30 sessions. The proportion of time allotted to headshakes remained unchanged in 10 sessions, and decreased in 11 sessions. In each regime, increases were (far) more common than decreases (tab. 5.3.2-4). While increases roughly equalled 'no change' with respect to FAs-B_1 (9 vs. 7), they were far more common than 'no change' in FAs subjected to the other 3 regimes ($C_{1,2}$: 10 vs. 0, X: 6 vs. 3, and Y: 5 vs. 0). As for FAs-X, decreases equalled 'no change' (3 vs. 3).

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-11) in proportions of 'time spent performing headshakes' between pre- and during-visitation amounted to +0.20 % (range: -4 % to +3 %).

Pooled by regime (appendix 5.3.2-3.06), response levels per session were most pronounced at FAs-Y, with a median of differences of +0.45 % (range: -0.70 % to +2 %), followed by FAs-$C_{1,2}$ (MoD: +0.25 %; range: -4 % to +3 %) and FAs-B_1 (MoD: +0.20 %; range: -2 % to +2 %). The MoD was least pronounced at FAs-X (+0.10 %; range: -0.80 % to +1 %).

Between the periods **during and after** human visitation, the difference in proportion of time spent performing headshakes analysed for ***all regimes*** together was not significant (pair-wise Friedman-test during-visit vs. post-visit: χ^2=1.089, p=0.297; tab. 5.3.2-3), indicating that visitor withdrawal did not result in a pronounced cessation of response (difference in medians: -0.20 %; tab. 5.3.2-11).

With respect to ***individual regimes*** (appendix 5.3.2-3.05), the difference in medians was 'highest' at FAs-$C_{1,2}$ (decrease by -0.35 %), followed by FAs-Y (decrease by -0.15 %), and lower again at FAs-B_1 (decrease by -0.05 %) and FAs-X (increase by +0.05 %).

As for ***individual sessions*** (tab. 5.3.2-4), post-visit proportions of headshakes increased (as compared to during-visit) in 19 sessions. They remained unchanged in 6 sessions, and decreased in 26 sessions.

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-11) in proportions of 'time spent performing headshakes' between during- and post-visitation amounted to a mere -0.06 % (range: -3 % to +3 %).

Pooled by regime (appendix 5.3.2-3.06), response levels per session were most pronounced at FAs-Y, with a median of differences of -0.30 % (range: -1 % to +1 %), followed by FAs-$C_{1,2}$ (MoD: -0.20 %; range: -3 % to +2 %). The median of differences was next to nonexistent at FAs-X (-0.05 %; range: -2 % to +3 %); it amounted to zero at FAs-B_1 (MoD: 0 %; range: -1 % to +2 %).

With respect to the periods **before and after** human visitation, pair-wise Friedman-test indicated a 'weakly'[2] significant difference between proportions of headshakes calculated for ***all regimes*** (χ^2=4.333, p=0.037; tab. 5.3.2-3), with difference in medians at +0.20 % (tab. 5.3.2-11). As regards prevalence of headshakes, overall response suggests that recovery was more or less effected.

Looking at ***individual regimes*** (appendix 5.3.2-3.05), median post-visit values for headshakes were above those found before human visitation in FAs-B_1, FAs-X, and FAs-Y, but were approximately equal at FAs-$C_{1,2}$, resulting in the least pronounced difference in medians at that regime (decrease by -0.05 %). Increases were most pronounced at FAs-Y (by +0.40 %), and considerably lower at FAs-B_1 and FAs-X (increases by +0.15 % and +0.10 %, resp.).

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[2] i.e., the significance does not survive sequential Bonferroni corrections

As for ***individual sessions*** (tab. 5.3.2-4), post-visit proportions of time spent performing headshakes increased (as compared to pre-visit) in 26 sessions, remained unchanged in 12 sessions, and decreased in 13 sessions. Of the latter, the post-visit decrease constituted a 'continuation' in 4 sessions, in that during-visit proportions had already been lower than pre-visit proportions (appendix 5.3.2-3.01). In three of these, headshakes had been comparatively common prior to visitation (2 %, 2 %, 1 %), while in the fourth, the proportion had been below 1 % (0.5 %). A continuous increase was observed in 7 sessions, in five of which headshakes had not at all been observed prior to visitation. In the remaining 2 sessions, they had been below 1 % (0.2 % and 0.5 %, resp.). With the exception of FAs-$C_{1,2}$ (8 vs. 7 sessions), increases were (far) more common than decreases (tab. 5.3.2-4).

In 51 % of all sessions, post-visit proportions of time spent performing headshakes remained higher than pre-visit proportions, while in 25 %, they were lower than observed prior to visitation.

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-11) in proportions of time spent performing headshakes between pre- and post-visitation amounted to +0.10 % (range: -3 % to +3 %).

Pooled by regime (appendix 5.3.2-3.06), **extent of recovery** found within each session was 'least effected' at FAs-B_1, with a median of differences of +0.15 % (range: -2 % to +3 %), followed by FAs-X (MoD: +0.10 %; range: -0.90 % to +3 %), and approximately completed for FAs-$C_{1,2}$ (MoD: +0.05 %; range: -3 % to +2 %) and FAs-Y (MoD: +0.05 %; range: -0.20 % to +2 %).

5.3.2.1.10 Posture: 'Prone'

For ***all regimes*** together, proportions of **pre-visit time spent 'prone'** ranged from 0 % to 100 % (median: 100 %; tab. 5.3.2-12).

At ***individual regimes*** (fig. 5.3.2-7), median proportions of pre-visit time spent 'prone' were marginally lower at FAs-$C_{1,2}$ and FAs-X (99 %), than at FAs-B_1 and FAs-Y (100 %).

Looking at ***all regimes*** together, the proportion of time spent 'prone' differed significantly **among the three periods** (global Friedman-test: χ^2=9.950, p=0.007; tab. 5.3.2-3): During-visit proportions (95 %) were smaller than pre-visit proportions (100 %), while post-visit proportions (98 %) were slightly smaller than pre-, but greater than during-visit ones (tab. 5.3.2-12).

Table 5.3.2-12: Time Spent in Posture 'Prone' – Descriptive Statistics for Periods and Between-Period Differences. For between-period differences, positive values represent increases, negative values represent decreases. **N.b.:** Minimum negative values represent most pronounced decrease, and maximum negative values constitute least pronounced decrease. pre: prior to visitation, during: during visitation, post: after visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y); min.: minimum, Q 1: 1st quartile (25 %), Q 3: 3rd quartile (75 %), max.: maximum. Between-period differences include MoD-values (median of differences); DiM-values (difference in median) are attained by subtracting pre- from dur-, dur- from post-, and pre- from post-visit values, resp.

Comportment Parameter	Period/ Between-Period Difference		FAs-allReg				
			min.	Q 1	**median**	Q 3	max.
Posture: 'prone'	Period	pre	0.00	94.75	**100.00**	100.00	100.00
		during	24.50	83.30	**94.60**	100.00	100.00
		post	0.00	87.20	**98.00**	100.00	100.00
	Between-Period Difference	pre to during	-66.50	-14.75	**-1.00**	0.00	93.00
		during to post	-89.90	-2.60	**0.60**	12.60	53.10
		pre to post	-100.00	-7.90	**0.00**	0.90	97.60

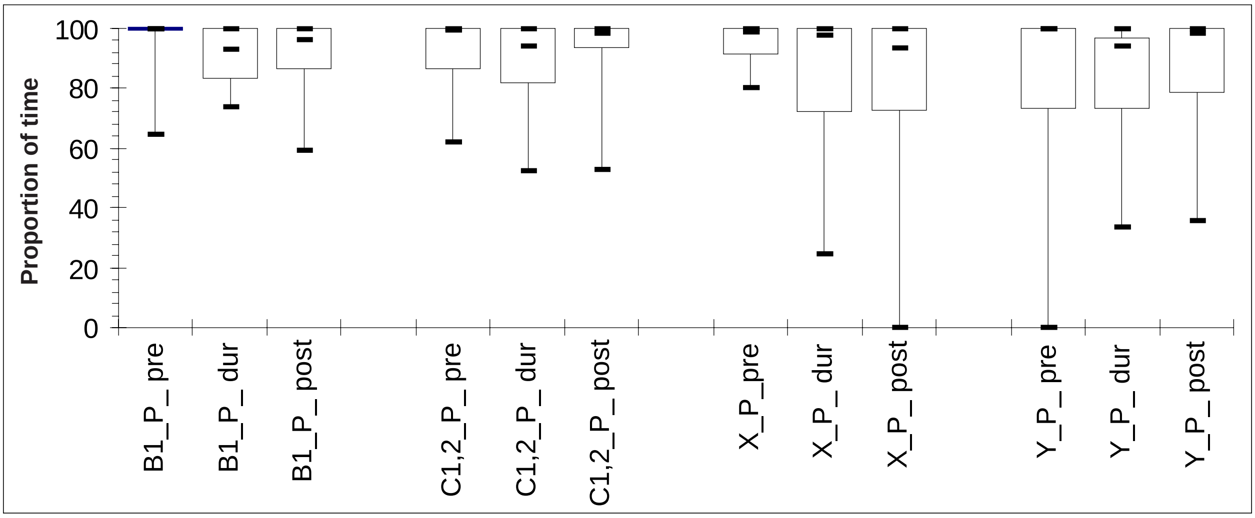

Figure 5.3.2-7: Proportion of Time Spent 'Prone' before, during, and after Human Visitation. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; _P = time spent 'prone'; pre = pre-visit, dur = during-visit, post = post-visit. Boxplot-values depict minimum, 25 %, median, 75 %, and maximum for each regime.

Figure 5.3.2-7 shows changes between periods found at ***individual regimes***: While FAs-B_1, FAs-$C_{1,2}$, and FAs-Y exhibited the basic pattern described above, FAs-X were unique in that post-visit proportions were lower than during-visit ones. Boxplots also indicate that pre-visit proportions, as well as the extent of response and recovery were different in ***individual sessions***.

Comparing the periods **before and during** human visitation, the proportion of time spent 'prone' decreased (difference in medians: -5 %; tab. 5.3.2-12) in the latter for ***all regimes***. Pair-wise Friedman-test indicated a significant difference (pre-visit vs. during-visit: χ^2=8.526, p=0.004; tab. 5.3.2-3), suggesting that visitor presence and action resulted in a distinct overall response.

Looking at ***individual regimes*** (appendix 5.3.2-3.05), the difference in medians was highest at FAs-B_1 (decrease by -7 %), followed by FAs-Y and FAs-$C_{1,2}$ (decreases by -6 % and -5 %, resp.), and least pronounced at FAs-X (decrease by only -0.85 %).

As for ***individual sessions***, an increase in time spent 'prone' from before to during visitation was found in 10 sessions. The proportion remained unchanged in 13 sessions, and decreased in 28 sessions. Regardless of regime, decreases were more commonly observed than increases (tab. 5.3.2-5).

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-12) in proportions of time spent 'prone' between pre- and during-visitation amounted to -1 % (range: -67 % to +93 %).

Pooled by regime (appendix 5.3.2-3.06), response levels per session were most pronounced at FAs-Y with a MoD-value of -4 % (range: -67 % to +93 %), followed by FAs-B_1 (MoD: -2%; range: -26 % to +26 %). Medians of differences were negligible at FAs-X (-0.60 %; range: -65 % to +17 %), and FAs-$C_{1,2}$ (MoD: -0.50 %; range: -48 % to +34 %), even though range indicated that individual responses in either direction, but particularly decreases in time spent 'prone', had been quite distinct.

Between the periods **during and after** human visitation, the difference in proportion of time spent 'prone' calculated for ***all regimes*** together was not significant (pair-wise Friedman-test during-visit vs. post-visit: χ^2=3.429, p=0.064; tab. 5.3.2-3), indicating that visitor withdrawal did not result in a pronounced cessation of response (difference in medians: +3 %; tab. 5.3.2-12).

With respect to ***individual regimes*** (appendix 5.3.2-3.05), median post-visit proportion of time spent 'prone' increased (as compared to during-visit) resulting in positive DiM-values (difference-in-median) for FAs-B_1, FAs-$C_{1,2}$, and FAs-Y, while FAs-X 'made up for the lack of response' shown previously by exhibiting a median decrease of -5 %. Concerning increases, DiM-values approximated +4 % at FAs-$C_{1,2}$ and FAs-Y; the value was slightly lower at FAs-B_1 (+3 %).

As for ***individual sessions***, post-visit proportions of time spent 'prone' increased (as compared to during-visit) in 27 sessions. They remained unchanged in 9 sessions, and decreased in 15 sessions (tab. 5.3.2-5). Increases equalled decreases at FAs-B_1, and were more common than decreases with respect to FAs-$C_{1,2}$, FAs-X, and FAs-Y.

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-12) in proportions of time spent 'prone' between during- and post-visitation amounted to +0.60 % (range: -90 % to +53 %).

Pooled by regime (appendix 5.3.2-3.06), response levels per session were most pronounced at FAs-$C_{1,2}$ (range: -41 % to +43 %) and FAs-Y (range: -2 % to +13 %), with medians of differences of +3 %. Medians of differences were negligible at FAs-X (MoD: +0.15 %; range: -90 % to +53 %), and amounted to zero at FAs-B_1 (MoD: 0 %; range: -39 % to +26 %) even though range indicated that individual responses in either direction (particularly decreases) had been quite distinct.

As regards the periods **before and after** human visitation, pair-wise Friedman-test did not indicate a significant difference between proportions of time spent 'prone' calculated for ***all regimes*** (χ^2=1.778, p=0.182; tab. 5.3.2-3), with difference in medians at -2 % (tab. 5.3.2-12). With respect to time spent 'prone', overall response suggested that recovery was more or less effected.

Looking at ***individual regimes*** (appendix 5.3.2-3.05), median post-visit proportions of time spent 'prone' remained (just) below those found before human visitation at each of the regimes. The difference in medians was little pronounced for FAs-$C_{1,2}$ (decrease by -0.80 %) and FAs-Y (decrease by -1 %), more pronounced for FAs-B_1 (decrease by -4 %), and most pronounced for FAs-X (decrease by -6 %).

As for ***individual sessions***, post-visit proportions of time spent 'prone' decreased in 22 sessions (as compared to pre-visit). They remained unchanged in 15 sessions, and increased in 14 sessions (tab. 5.3.2-5). A continuous decrease was observed in 4 sessions, for all of which pre-visit proportions had invariably been at 100 %. Post-visit, but not necessarily during-visit, continuous decreases in time spent 'prone' coincided with increases in either comfort (2 sessions; post-visit proportions of 5 % and 79 %, resp.) or breeding behaviour (2 sessions; post-visit proportions of 24 % and 47 %, resp.). A continuous increase in time spent 'prone' was found in 3 sessions (appendix 5.3.2-3.01), with very different pre-visit proportions, viz., 0 %, 62 %, and 80%, respectively. In the lattermost, pre-visit proportions for breeding behaviour had amounted to 20 %, while in the former two, (very) high pre-visit proportions for comfort behaviour had been calculated (67 % and 14 %, resp.).

In 43 % of all sessions, post-visit proportions of time spent 'prone' remained lower than pre-visit proportions, while in 27 %, they were higher than observed prior to visitation.

The median of differences (MoD; magnitude of within-session response across all sessions of all regimes; tab. 5.3.2-12) in proportions of time spent 'prone' between pre- and post-visitation amounted to zero (MoD: 0 %; range: -100 % to +98 %).

Pooled by regime (appendix 5.3.2-3.06), **extent of recovery** found within each session was least pronounced at FAs-X, with a MoD-value of -4 % (range: -100 % to +20 %). MoD-values amounted to zero at FAs-B_1 (MoD: 0 %; range: -35 % to +22 %), FAs-$C_{1,2}$ (MoD: 0 %; range: -36 % to +38 %), and FAs-Y (MoD: 0 %; range: -64 % to +98 %).

5.3.2.1.11 Regime Differences as Detected by Quantitative Comparisons

Recapitulation: In terms of severity, loud and fast visitation (L&F) is hypothesised to exceed impact of silent and slow visitation (S&S), while 3 visitors (3 P) are assumed to exert a greater impact than 1 visitor (1 P). Ranking the regimes employed in this study, the following order would ensue:

3 P, L&F (FAs-Y) > 1 P, L&F (FAs-B_1; FAs-C_2) $\geq$ 3 P, S&S (FAs-X) > 1 P, S&S (FAs-C_1)

N.b.: In the text, FAs-$C_{1,2}$ will be summarily referred to as having been subjected to 'predominantly the regime 1 P, S&S', as next to no difference in comportment had been observed in the first session following the switch in regimes (to 1 P, L&F).

Whereas rankings during visual appraisal (section 5.3.3; q.v.) examined consistency of response among penguins subjected to a given visiting regime (key question: How many?), quantitative comparisons offered the possibility of ranking regimes in accordance with *differences in median* (DiM; between the periods pre-, during- and post-visit; tab. 5.3.2-13, tab. 5.3.2-14; ***all sessions*** from FAs subjected to a given regime) as well as with *median of differences* (MoD; between the periods pre-, during- and post-visit; tab. 5.3.2-15, tab. 5.3.2-16) in response found in ***individual sessions*** (two ways of asking the key question 'How much'?). For this, responses obtained from FAs subjected to the different regimes were ranked according to magnitude of these two key values (tab. 5.3.2-13, tab. 5.3.2-15). Additionally, tables 5.3.1-14 and 5.3.2-16 display summed up rank positions (for each of the four ranks) across all parameters analysed.

N.b.: Values between and excluding -1.00 and +1.00 are sorted with 0 ('no change'), except for the least time-consuming parameter, viz., headshakes, for which values between and excluding -0.10 and +0.10 are assigned to this category.

With respect to *differences in median* (tab. 5.3.2-13), regime-mediated rank orders in magnitude of responses from **pre- to during-**visitation were observed as regards the parameters 'rest' (decrease) and 'vigilance' (increase), while conduct-mediated responses (FAs subjected to loud and fast regimes responding more strongly than those experiencing silent and slow visitations) were additionally found for the parameters 'breed' (increase) and 'posture – prone' (decrease). From **during- to post-**visitation, rank orders did not tally with hypothesised severity of regime or visitor conduct for any of the parameters examined. Comparing the periods of **pre- and post-**visitation, increased occurrence of headshakes was in line with hypothesised differences in severity of regimes, while increased breeding behaviour appeared conduct-mediated.

As regards the *median of differences* (tab. 5.3.2-15) from **pre- to during-**visitation, regime-mediated rank orders in magnitude of responses were observed with respect to the parameters 'rest' (decrease) and 'vigilance' (increase), while a conduct-mediated response was additionally found for the parameter 'posture – prone' (decrease). As with differences in medians, rank orders from **during- to post-**visitation did not tally with hypothesised severity of regime or conduct for any of the parameters examined. Comparing the periods of **pre- and post-**visitation, decreased resting behaviour and increased vigilance corresponded to hypothesised differences in severity of regimes; additionally, increased breeding behaviour appeared conduct-mediated.

Table 5.3.2-13: Ranked Regime Differences in Magnitudes of Difference in (Period) Medians (DiM). As colour codes for change classes (cf. 5.3.1, 5.3.3) do not apply here, values in **bold red** indicate rank order in concordance with hypothesised differences in severity of regime; values in red suggest conduct-mediated response differences. Values between and excluding -1.00 and +1.00 are sorted with 0 ('no change'), except for the least time-consuming parameter, viz., headshakes, for which values between and excluding -0.10 and +0.10 are assigned to this category. during minus pre: pre-visit median value subtracted from during-visit median value; post minus during: during-visit median value subtracted from post-visit median value; post minus pre: pre-visit median value subtracted from post-visit median value; -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

	Parameter	-4	-3	-2	-1	0	+1	+2	+3	+4
during minus pre	rest	**Y**	**B_1**	**X**	**$C_{1,2}$**					
	comfort					Y; B_1; X; $C_{1,2}$				
	breed					X; $C_{1,2}$			B_1	Y
	vigilance						**$C_{1,2}$**	**B_1**	**X**	**Y**
	agonistics					B_1; $C_{1,2}$			X	Y
	headshakes					X		B_1	$C_{1,2}$	Y
	posture prone	B_1	Y	$C_{1,2}$		X				
post minus during	rest						$C_{1,2}$	Y	X	B_1
	comfort					Y; B_1; X; $C_{1,2}$				
	breed	Y				B_1; X; $C_{1,2}$				
	vigilance	B_1	X	Y	$C_{1,2}$					
	agonistics	X				B_1; $C_{1,2}$				Y
	headshakes	$C_{1,2}$	Y			B_1; X				
	posture prone	X						B_1	$C_{1,2}$	Y
post minus pre	rest	Y	X	$C_{1,2}$	B_1					
	comfort					Y; B_1; X; $C_{1,2}$				
	breed	X				$C_{1,2}$			B_1	Y
	vigilance					B_1		X	$C_{1,2}$	Y
	agonistics					B_1; X; $C_{1,2}$				Y
	headshakes					**$C_{1,2}$**		**X**	**B_1**	**Y**
	posture prone	X	B_1	Y		$C_{1,2}$				

Table 5.3.2-14: Ranked Responses in Magnitudes of Difference in Medians (DiM) Between Periods Summed Up Per Rank Position For Each Visiting Regime. Values depict sums for overall response magnitudes (tot), and for response magnitudes from pre- to during-visitation (dur - pre), from during- to post-visitation (post - dur), and from pre- to post-visitation (post – pre) per rank position. ±4 to ±1: ranked from most to least pronounced, FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

rank	**+/-4**				**+/-3**				**+/-2**				**+/-1**			
FA	Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$
tot	**13**	**3**	**4**	**1**	**2**	**5**	**5**	**3**	**3**	**3**	**3**	**2**	**0**	**1**	**0**	**4**
dur - pre	5	1	0	0	1	2	2	1	0	2	1	1	0	0	0	2
post - dur	3	2	2	1	1	0	2	1	2	1	0	0	0	0	0	0
post - pre	5	0	2	0	0	3	1	1	1	0	2	1	0	1	0	0

'Rank 0'-values: Y: 3; B_1: 9, X: 9, $C_{1,2}$: 11

Table 5.3.2-15: Ranked Regime Differences in Magnitudes of Median of Differences (MoD). As colour codes for change classes (cf. 5.3.1, 5.3.3) do not apply here, values in **bold red** indicate rank order in concordance with hypothesised differences in severity of regime; values in red suggest conduct-mediated response differences. Values between and excluding -1.00 and +1.00 are sorted with 0 ('no change'), except for the least time-consuming comportment parameter, viz., headshakes, for which values between and excluding -0.10 and +0.10 are assigned to this category. during minus pre: pre-visit MoD-value subtracted from during-visit MoD-value; post minus during: during-visit MoD-value subtracted from post-visit MoD-value; post minus pre: pre-visit MoD-value subtracted from post-visit MoD-value; -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase.

	Parameter	**-4**	**-3**	**-2**	**-1**	**0**	**1**	**2**	**3**	**4**
during minus pre	rest	**Y**	**X**	**B_1**	**$C_{1,2}$**					
	comfort					Y; B_1; X; $C_{1,2}$				
	breed	X				B_1; $C_{1,2}$				Y
	vigilance						**$C_{1,2}$**	**X**	**B_1**	**Y**
	agonistics					B_1; X			$C_{1,2}$	Y
	headshakes						X	B_1	$C_{1,2}$	Y
	posture prone	Y	B1			X; $C_{1,2}$				
post minus during	rest						Y	$C_{1,2}$	X	B_1
	comfort					Y; B_1; X; $C_{1,2}$				
	breed					B_1; X; $C_{1,2}$				Y
	vigilance	B_1	X	$C_{1,2}$	Y					
	agonistics					Y; B_1; X; $C_{1,2}$				
	headshakes	Y	$C_{1,2}$			B_1; X				
	posture prone					B_1; X			$C_{1,2}$	Y
post minus pre	rest	**Y**	**X**	**B_1**	**$C_{1,2}$**					
	comfort					Y; B_1; X; $C_{1,2}$				
	breed					X; $C_{1,2}$			B_1	Y
	vigilance						**$C_{1,2}$**	**B_1**	**X**	**Y**
	agonistics					Y; B_1; X				$C_{1,2}$
	headshakes					Y; $C_{1,2}$			X	B_1
	posture prone	X				Y; B_1; $C_{1,2}$				

Table 5.3.2-16: Ranked Responses in Magnitudes of Median of Differences (MoD). Summed Up Per Rank Position For Each Visiting Regime. Values depict sums for overall response magnitudes (tot), and for response magnitudes from pre- to during-visitation (dur - pre), from during- to post-visitation (post - dur), and from pre- to post-visitation (post – pre) per rank position. ±4 to ±1: ranked from most to least pronounced, FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

rank	**+/-4**				**+/-3**				**+/-2**				**+/-1**			
FA	Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$	Y	B_1	X	$C_{1,2}$
tot	**12**	**3**	**2**	**1**	**0**	**3**	**6**	**4**	**0**	**4**	**1**	**2**	**2**	**0**	**1**	**4**
dur - pre	6	0	1	0	0	2	1	2	0	2	1	0	0	0	1	2
post - dur	3	2	0	0	0	0	2	2	0	0	0	2	2	0	0	0
post - pre	3	1	1	1	0	1	3	0	0	2	0	0	0	0	0	2

'Rank 0'-values: Y: 7, B_1: 11, X: 11, $C_{1,2}$: 10

Looking at *summed up rank positions* for both key values, summed up ranks for differences in medians (tab. 5.3.2-14) reliably distinguish between most and least severe regimes (FAs-Y, 3 P, L&F vs. FAs-C$_{1,2}$, predominantly 1 P, S&S), which always retain highest sums of most (±4) and least (±1, particularly, if the 'rank' for zero response difference is included) pronounced ranks, respectively. As regards median of differences (tab. 5.3.2-16), *summed up rank positions* reliably identify the most severe regime (3 P, L&F); additionally, they position the least severe regime (1 P, S&S) on the least pronounced rank with one exception, viz., median of differences from **during- to post-**visitation (for which ‘highest’ number of least pronounced responses falls to FAs-Y). Neither key value exhibits sensitivity with respect to the middle ranks (±2, ±3).

Given the **statistic property of median values** (i.e., relative robustness towards deviations), these results stress that the regimes hypothesised to represent the most and least severe in terms of impact elicit a substantial unity with respect to intensity of behavioural changes across comportment parameters.

5.3.2.2 Variation in Heart Rate before, during, and after Human Visitation Compared to Variation in Heart Rate Obtained in Successive ‘Baseline’-Intervals

N.b.: Outside visitation[3] , there was no such thing as consistent ‘individual heart rate’ across sessions, even though the greater part of locomotor heart rate had been eliminated by using artificial eggs. Neither could variation be attributed to climatic conditions, as heart rate from different focal animals recorded on the same day and at the same location also showed substantial differences.

Within each session, heart rate of resting penguins could be demonstrated to ‘undulate regularly’ (section 5.3.1; q.v.); higher amplitudes and abrupt changes were assumed to result from disturbance.

To test this assumption, analysis of heart rate variation was extended to not only include *‘visited’* sessions but also so-called *‘baseline’* sessions, i.e. sessions without human visitation. This way, it was possible to not only examine heart rate variation across periods (before, during, and after human visitation; approx. 10 min in duration), but to additionally compare this variation with variation recorded for successive 10 min-intervals without human interference.

Recapitulation: Heart rate is defined to ‘undulate regularly’ if values from successive 20 s-counts differ by one or two beats without, however, resulting in a trend (increase/ decrease). These ‘undulations’ are considered ‘physiologically normal’.

Data presented in this section are based on 67 sessions (30 ‘visited’, 37 ‘baseline’) from 16 FAs (of which 10 ‘visited’ and ‘baseline’, 6 ‘baseline’ only; tab. 5.3.2-17).

Table 5.3.2-17: Database Used for Comparison of Heart Rate Variation. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-A, FAs-B_1, FAs-$C_{1,2}$, FAs-X, FAs-Y). FAs-A: never visited; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F.

Regime		FAs-allReg	FAs-A	FAs-B_1	FAs-$C_{1,2}$	FAs-X	FAs-Y
Number of Sessions	'Visited'	30	0	11	11	5	3
	'Baseline'	37	11	6	5	9	6
Number of FAs	'Visited'	10	0	4	3	2	1
	'Baseline'	16	4	4	3	3	2

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[3] including ‘prior to’, as well as entire sessions without human visitation

5.3.2.2.1 Methodological Prelude

Recapitulation: During primary transcription of focal-animal heart rate, logger data (voltage files) had been transformed into counts of heartbeats per 20 s-interval and the resulting figures added to the Excel-matrix (every 20th second).

■ Secondary Transcriptions of Focal-Animal Heart Rate and Human Disturbance

Heart rate was analysed as beats-per-20 s values (real-time counts). All values obtained during a given period/ 10 min-interval were used for comparisons. Comparisons of heart rate variation were analysed using a total of 8 statistical parameters, viz., mean and standard deviation (SD), 1st and 3rd quartiles (Q 1; Q 3), minimum, median, maximum (min., med., max.), and range. These parameters were calculated for each period/ 10 min-interval.

As a rule, **overlaps**, i.e. heart rate values for which the 20 s count 'fell between' periods[4], were sorted with the following period. An exception was made if the previous period had contained more than 15 s of the counting-interval.

The Visiting Stage Performance Indicator Value (tab. 5.3.1-3; q.v.) served to distinguish the period of visitation from periods before and after the visit. *'Baseline'* sessions were simply divided into 10 min-intervals (truncated with respect to FAsX and FAsY, as original records had comprised 45 min).

Conspecific and **predator/ aircraft** disturbance do not feature in this section.

■ Presentation of Results

Tabulated results: Using Friedman-tests, consistency of directions of change was analysed for a total of 8 statistical parameters (tab. 5.3.2-18). The magnitude of between-period ('visited') and between-interval ('baseline') differences was compared by using pre-visit values/ values obtained in the 1st 'baseline'-interval as a reference. During- and post-visit values as well as values obtained in the 2nd and 3rd 'baseline'-intervals were subsequently tabulated as a proportion of these values to compare their respective deviations (tab. 5.3.2-19; tab. 5.3.2-20).

Figures: Scatterplots are provided to visualise magnitudes of between-period and between-interval differences in each statistical parameter for *'visited'* and *'baseline'* sessions, respectively (fig. 5.3.2-8 a-h).

Colour code: The colour code used to facilitate visual discrimination of significance levels has been introduced in the chapter Materials and Methods and repeated at the beginning of the beginning of the results chapter (tab. 5.1-3; q.v.).

Order of Presentation: In the ensuing section, Friedman-test results on consistency of direction of change are presented first. Following, between-period comparisons of heart rate (pre-, during-post-visit) and between-interval comparisons (1st, 2nd, and 3rd 'baseline'-intervals) are presented. The magnitude of difference is focused upon in the last subsection.

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[4] As 10 min-intervals invariably started at second 01 of a given minute, and heart rate values were obtained for three 20 s-intervals per minute, overlaps did not feature with respect to 'baseline' sessions.

5.3.2.2.2 Interim Summary – Results on Variation in Heart Rate

Summing up, this section set out to address the question whether heart rate variation changed during human visitation, and intended to compare detected changes to 'natural fluctuations' over a similar interval of time outside visitation ('baseline' sessions).

Friedman-test showed significant **among-period differences** ('visited' sessions) for five of eight statistical parameters examined, whereas only two parameters attained statistical significance with respect to **among-interval differences** of *'baseline'* sessions.

Values of all eight statistical parameters of heart rate considerably deviated from pre-visit 'baseline' **during** visitation. They were 'more condensed' (i.e., they occupied fewer categories above the one containing 100 %, with very little change observed as regards categories below that) **after** than during visitation, but extent of variation was still more pronounced than pre-visit. In particular, maximum heart rate values post-visit continued to occupy higher categories than the other parameters. The observed pattern in '*visited*' sessions (during- and post-visit) was distinct from that found for '*baseline*' sessions both in the **2nd** and **3rd 'baseline'-intervals**; even post-visit, all heart rate parameters calculated for '*visited*' sessions still reached higher classes than their **'***baseline***'** session equivalents.

During the **3rd 'baseline'-interval**, values of statistical parameters for '*baseline*' sessions were more 'condensed' than in the **2nd interval** with respect to categories above 100 %. In contrast, little change in magnitude (Q 3 only) was observed concerning categories below 100 %.

With respect to the parameters 'standard deviation' and 'range', a wide 'scattering' of values was found for *'visited'* and *'baseline'* sessions alike. The observed patterns, however, were strikingly different when the period of visitation was compared to the **2nd 'baseline'-interval**: **During** visitation, the greatest part of variation in standard deviation as well as range was assigned to 'extreme' classes well above pre-visit levels, while a negligible part could be ascribed to variation 'extremely' below pre-visit levels. The opposite was true for the **2nd 'baseline'-interval**. In addition, a substantial part of *'baseline'* variation in range and standard deviation did indeed differ comparatively little from pre-visit levels. The greater similarity of patterns found when comparing the **post-visit** period to the **3rd 'baseline'-interval**, resulted from between-period changes in pattern in the *'visited'* sessions, while little between-interval change was observed in the *'baseline'* sessions.

5.3.2.2.3 Directions of Change among Periods/ 'Baseline'-Intervals

Heart rate records spanning all three periods[5] were available for 28 sessions during which human visitation had taken place. Additionally, heart rate from 34 'baseline' sessions during which humans had been entirely absent was examined. For these, a 30 min-session was divided into three equal parts.

Due to low number of sessions, Friedman-tests were only performed on ***all regimes*** (regime differences were not examined). Only global Friedman-tests were calculated, i.e., even in case of significant differences, no further splitting (pair-wise tests) was undertaken. In the ensuing subsections, information on Friedman-test mean ranks (tab. 5.3.2-18) is used in the text to indicate the most likely source of differences.

For both *'visited'* and *'baseline'* sessions, table 5.3.2-18 provides an overview of findings with respect to each statistical parameter.

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[5] Figures differ from those given in tab. 5.3.2-17 in that Friedman-tests for analysis of among-period/ among-interval differences did not include sessions for which values for only two of three periods/ 'baseline'-intervals were available.

5.3.2.2.4 Heart Rate Variation before, during, and after Human Visitation

For five of the eight statistical parameters analysed for ***all regimes*** together, global Friedman-tests showed significant differences **among the periods** (before, during, after visitation); additionally, one further parameter exhibited a tendency towards significance (tab. 5.3.2-18):

Taking the means of counted values for each period, Friedman-test showed significant differences (χ^2=7.714; p=0.021), with ‘during visitation’ ranking highest among the periods.

Concerning median values, these likewise ranked highest during visitation, but – possibly due to their greater robustness with respect to outliers – showed no more than a tendency towards significance (χ^2=5.460; p=0.065).

On the other hand, the difference between maximum values was ‘very highly’ significant (χ^2=16.491; p=0.000); and differences between 3rd quartile values were significant (χ^2=6.613; p=0.037), with highest rank again awarded to ‘during visitation’ for both statistical parameters.

Furthermore, the difference in standard deviations (χ^2=13.786; p=0.001) as well as the difference in range (χ^2=10.709; p=0.005) across periods were also highly significant, likewise suggesting greater fluctuations in heart rate during human visitation (highest rank) than during the other periods.

Neither minimum values nor 1st quartile values exhibited a significant difference among the periods.

These statistical findings tallied well with observations on ***individual sessions*** (see section 5.3.1), which showed that high heart rate rarely persisted throughout the visiting period, whereas an increased variation in heart rate was generally more prominent.

Table 5.3.2-18: Global Friedman-Test Results for Comparison of Heart Rate Variation per Period (‘Visited’ Sessions) and Heart Rate Variation per 10 min-Interval (‘Baseline’ Sessions). Variation represented by 8 parameters of descriptive statistics: mean, standard deviation (SD), 1st quartile (Q 1), minimum (min.), median (med.), maximum (max.), 3rd quartile (Q 3), range. rank: mean rank as calculated by Friedman-tests, pre: before, post: after; χ^2: Friedman-test statistic, Int.: ‘baseline’-interval. *Italics* indicate tendency towards significance. Underscored figures represent rank most likely responsible for significance.

all regimes 'visited' (28 sessions) pre-visit vs. during-visit vs. post-visit

heart rate statistic	χ^2	p	rank pre-visit	rank during-visit	rank post-visit
mean	7.714	0.021	1.79	2.43	1.79
SD	13.786	0.001	1.68	2.57	1.75
Q 1	0.528	0.768	1.93	2.11	1.96
min.	0.796	0.672	1.89	2.13	1.98
med.	5.460	*0.065*	1.80	2.34	1.86
max.	16.491	0.000	1.54	2.59	1.88
Q 3	6.613	0.037	1.77	2.39	1.84
range	10.709	0.005	1.73	2.50	1.77

all sessions 'baseline' (34 sessions) 01-10 min vs. 11-20 min vs. 21-30 min

heart rate statistic	χ^2	p	rank 1st Int.	rank 2nd Int.	rank 3rd Int.
mean	3.353	0.187	2.24	1.97	1.79
SD	2.824	0.244	2.24	1.88	1.88
Q 1	4.164	0.125	2.25	1.93	1.82
min.	8.017	0.018	2.35	1.93	1.72
med.	5.496	*0.064*	2.29	1.91	1.79
max.	7.215	0.027	2.18	2.19	1.63
Q 3	3.504	0.182	2.25	1.91	1.84
range	3.045	0.218	2.24	1.93	1.84

5.3.2.2.5 Heart Rate Variation across Successive ‘Baseline’-Intervals

To confirm that the differences found for the visiting period were not typical of just any record spanning 30 min, the same analyses were performed on *‘baseline’* sessions (sessions during which no visit had taken place).

For only two of the eight statistical parameters analysed for ***all regimes*** together, global Friedman-tests showed significant differences **among successive 10 min-intervals**; one further parameter exhibited a tendency towards significance (tab. 5.3.2-18): Mean values, standard deviations, 1st quartile and 3rd quartile values as well as range did not differ significantly across intervals.

Median values showed a tendency towards significance – again, possibly due to their greater robustness with respect to outliers – (χ^2=5.496; p=0.064), but contrary to visiting sessions, highest rank was assigned to the **1st ’baseline’-interval**.

Differences between maximum values were significant (χ^2=7.215; p=0.027), with fairly similarly ranked values for the **1st** and **2nd ’baseline’-intervals**, and a distinctly lower one for the **3rd interval**. Minimum values were also significantly different (χ^2=8.017; p=0.018), with the **1st ’baseline’-interval** ranking highest.

5.3.2.2.6 Comparison of Magnitudes of Heart Rate Variation – ‘Visited’ vs. ‘Baseline’ Sessions

Having confirmed that the ‘sticking out like a sore thumb’-quality of the visitation period in *‘visited’* session was not typical of 30-minute recording sessions in general, the focus was next set upon the **quantity of change** observed. To get a better understanding of the magnitude of differences between consecutive periods (for sessions including human visitation) and consecutive ‘baseline’-intervals, respectively, the extent of change had to be ‘earthed’.

For each session, **pre-visit** heart rate/ heart rate obtained during the **1st ’baseline’-interval** was taken to represent 100 % for all 8 statistical parameters (mean, standard deviation, etc.), and the changes found in the other periods (during- and post-visit) and 2nd and 3rd ‘baseline’-intervals were calculated as deviations from 100 %. Thus a decrease in, e.g., mean heart rate during visitation would result in a proportional value below 100 %, while an increase resulted in values exceeding 100 %.

The results were then scatterplotted separately for all *‘visited’* and all *‘baseline’* sessions (see fig. 5.3.2-8 a-h below), with Y-axis representing proportion and X-axis displaying consecutive periods/ intervals. The pre-visit period/ 1st ’baseline’-interval thus invariably contains only a single ‘dot’ at 100 %, while dots in the following periods/ ‘baseline’-intervals depict the amount of deviation found in each session. In the figures, interpolation lines have been added to aid interpretation.

The scatterplots (fig. 5.3.2-8 a-h) indicate a generally greater magnitude of **between-period differences** (‘visited’ sessions) as compared to **between-interval differences** (‘baseline’ sessions). Furthermore, the upward trend of the interpolation line found for all 8 statistical parameters in the period **‘during visitation’** does not appear with respect to the **2nd ’baseline’-interval**, except weakly for the parameter range. For maximum-values, a decreasing trend is indicated, while for the remaining statistical parameters no observable trend exists.

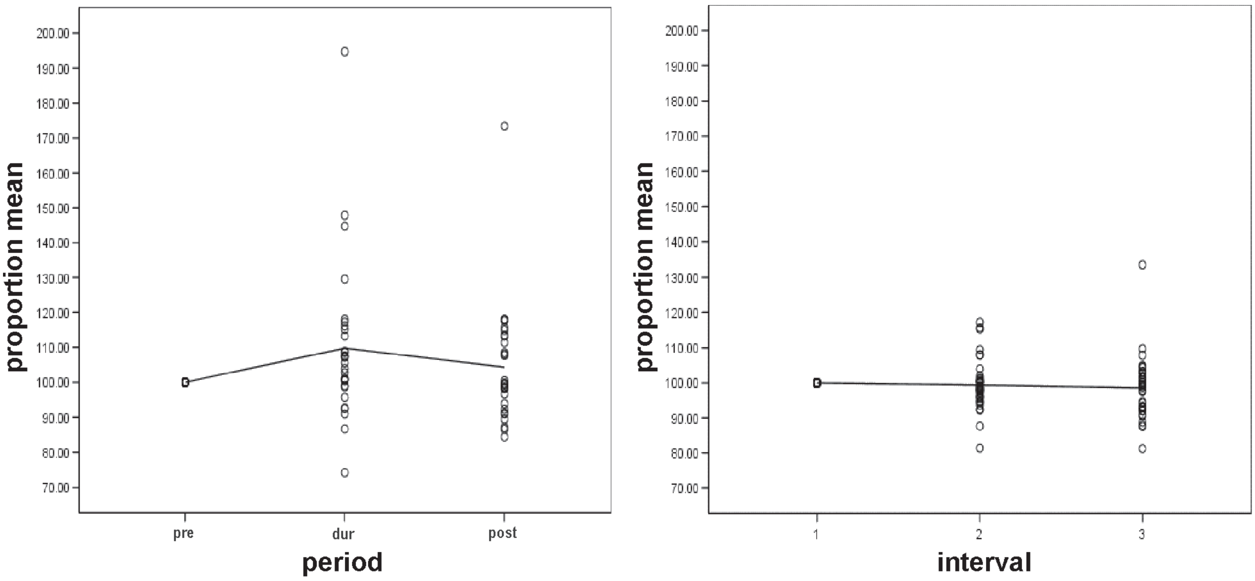

Figure 5.3.2-8 a: Proportional Changes in <u>Mean</u> Values of Heart Rate during Visit (left) and 'Baseline' (right) Sessions. Pre-visit values and values obtained for 1st 'baseline'-intervals have been set to 100 %, values for the following periods/ intervals are expressed as changes from 100 %. Dots represent proportional values for single sessions; line: interpolation line.

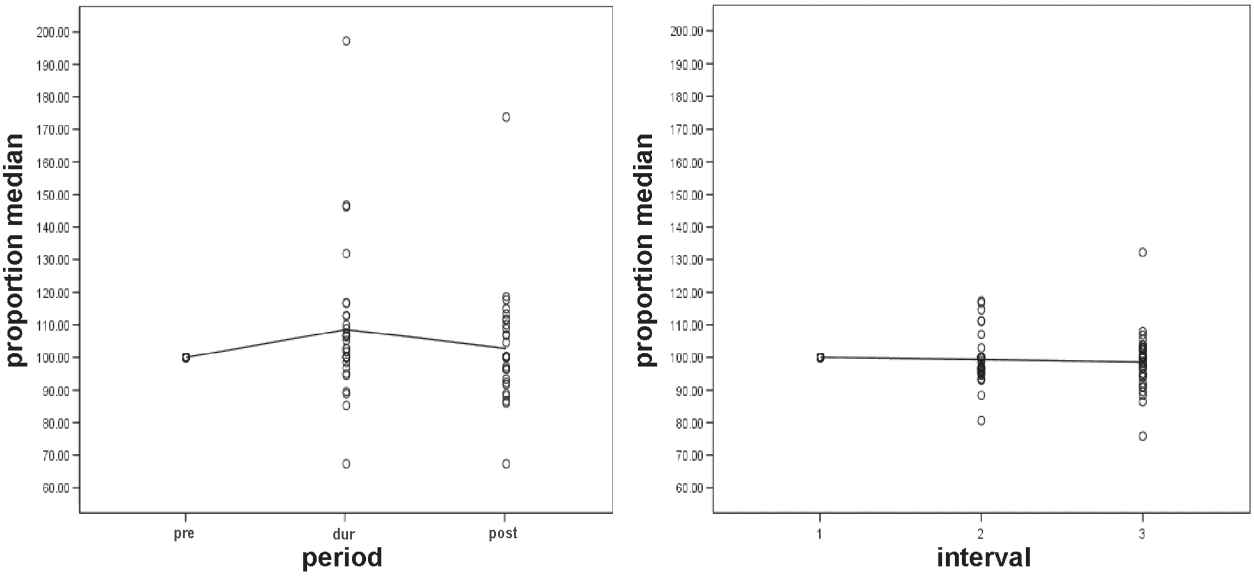

Figure 5.3.2-8 b: Proportional Changes in <u>Median</u> Values of Heart Rate during Visit (left) and 'Baseline' (right) Sessions. Pre-visit values and values obtained for 1st 'baseline'-intervals have been set to 100 %, values for the following periods/ intervals are expressed as changes from 100 %. Dots represent proportional values for single sessions; line: interpolation line.

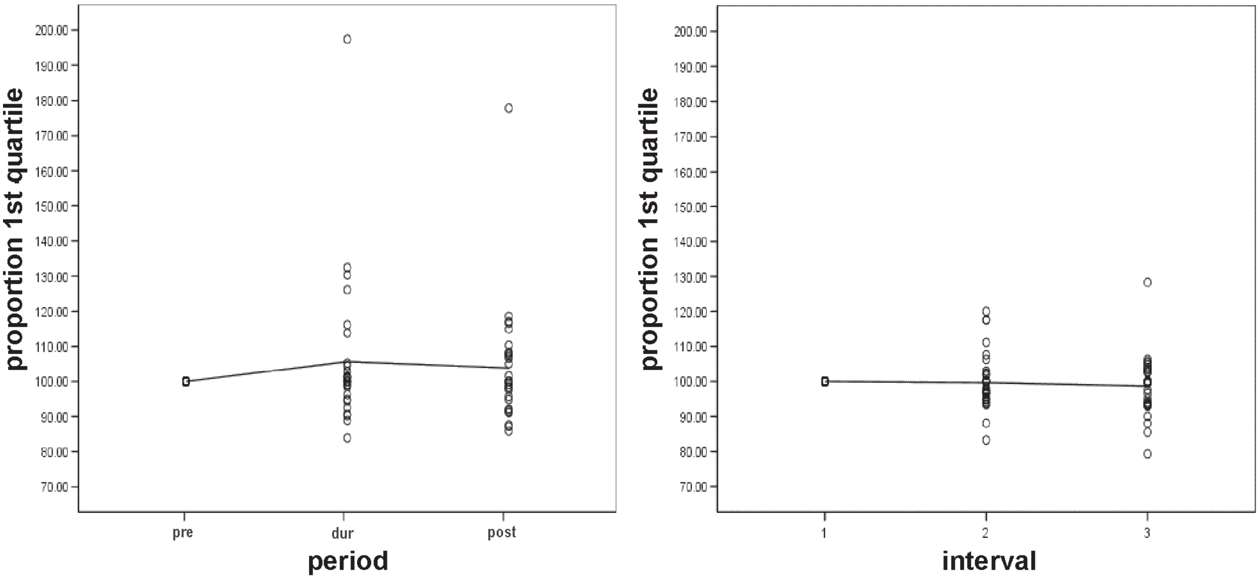

Figure 5.3.2-8 c: Proportional Changes in 1st Quartile Values of Heart Rate during Visit (left) and 'Baseline' (right) Sessions. Pre-visit values and values obtained for 1st 'baseline'-intervals have been set to 100 %, values for the following periods/ intervals are expressed as changes from 100 %. Dots represent proportional values for single sessions; line: interpolation line.

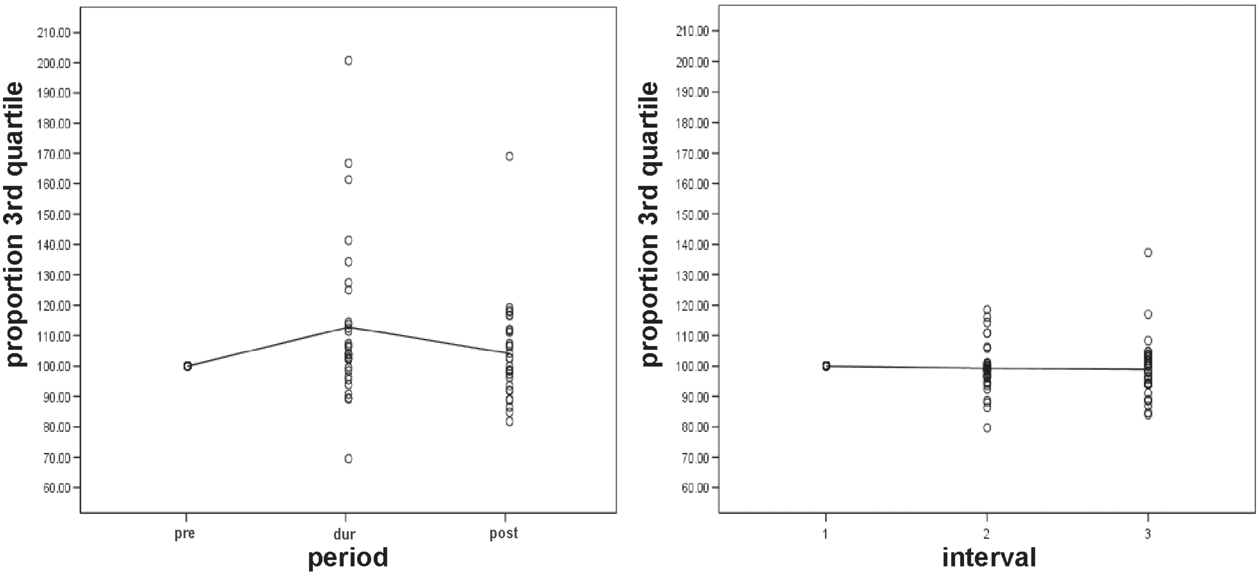

Figure 5.3.2-8 d: Proportional Changes in 3rd Quartile Values of Heart Rate during Visit (left) and 'Baseline' (right) Sessions. Pre-visit values and values obtained for 1st 'baseline'-intervals have been set to 100 %, values for the following periods/ intervals are expressed as changes from 100 %. Dots represent proportional values for single sessions; line: interpolation line.

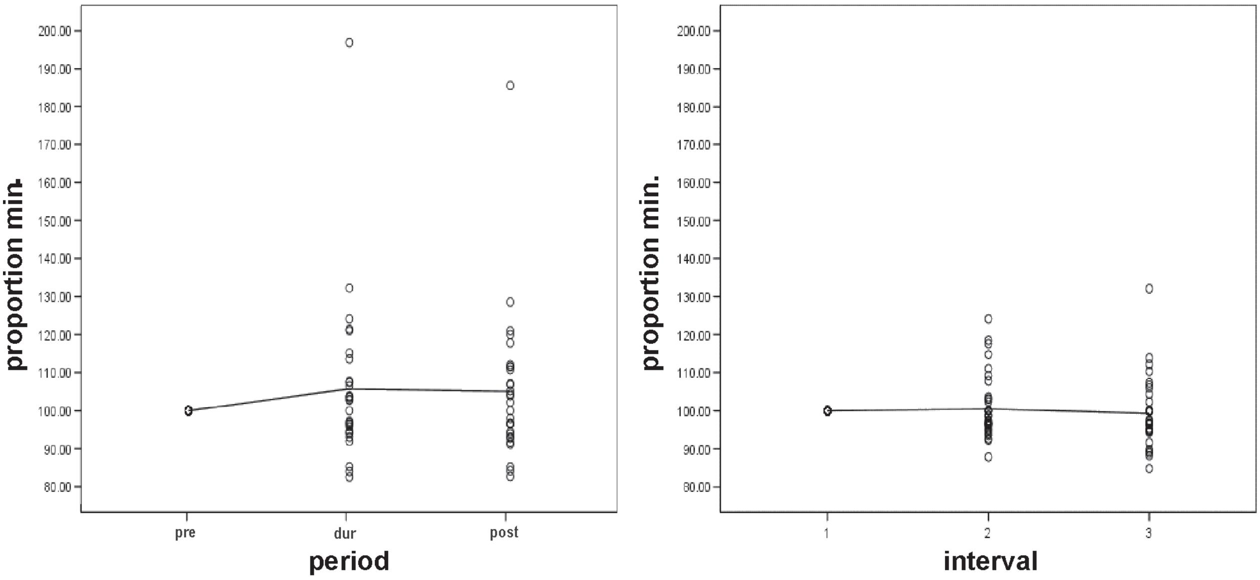

Figure 5.3.2-8 e: Proportional Changes in Minimum Values of Heart Rate during Visit (left) and 'Baseline' (right) Sessions. Pre-visit values and values obtained for 1st 'baseline'-intervals have been set to 100 %, values for the following periods/ intervals are expressed as changes from 100 %. Dots represent proportional values for single sessions; line: interpolation line.

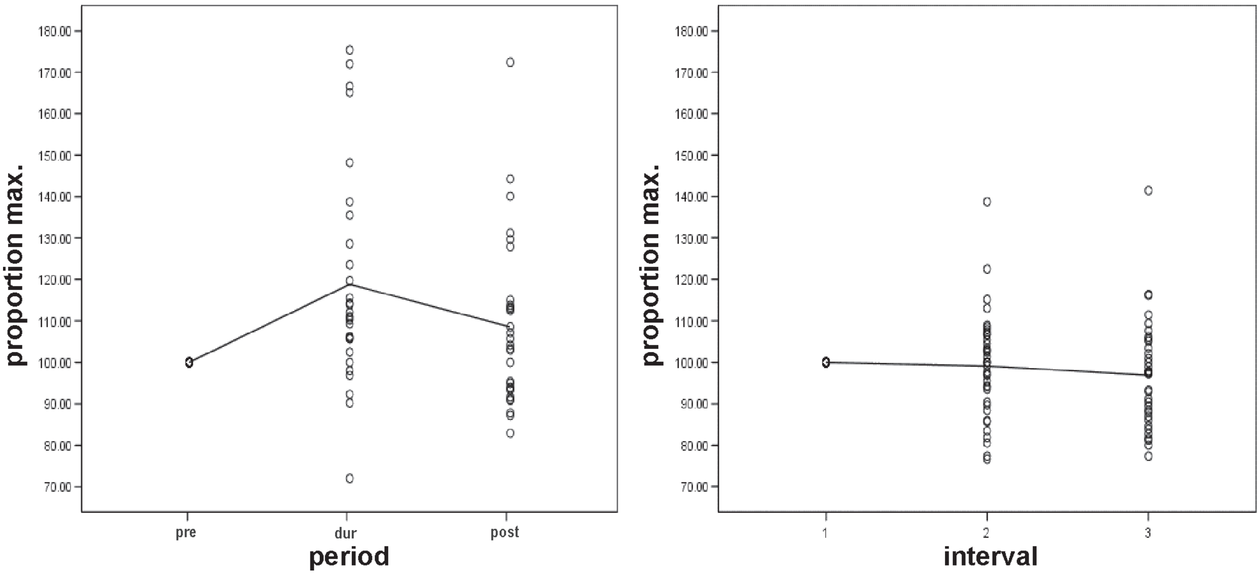

Figure 5.3.2-8 f: Proportional Changes in Maximum Values of Heart Rate during Visit (left) and 'Baseline' (right) Sessions. Pre-visit values and values obtained for 1st 'baseline'-intervals have been set to 100 %, values for the following periods/ intervals are expressed as changes from 100 %. Dots represent proportional values for single sessions; line: interpolation line.

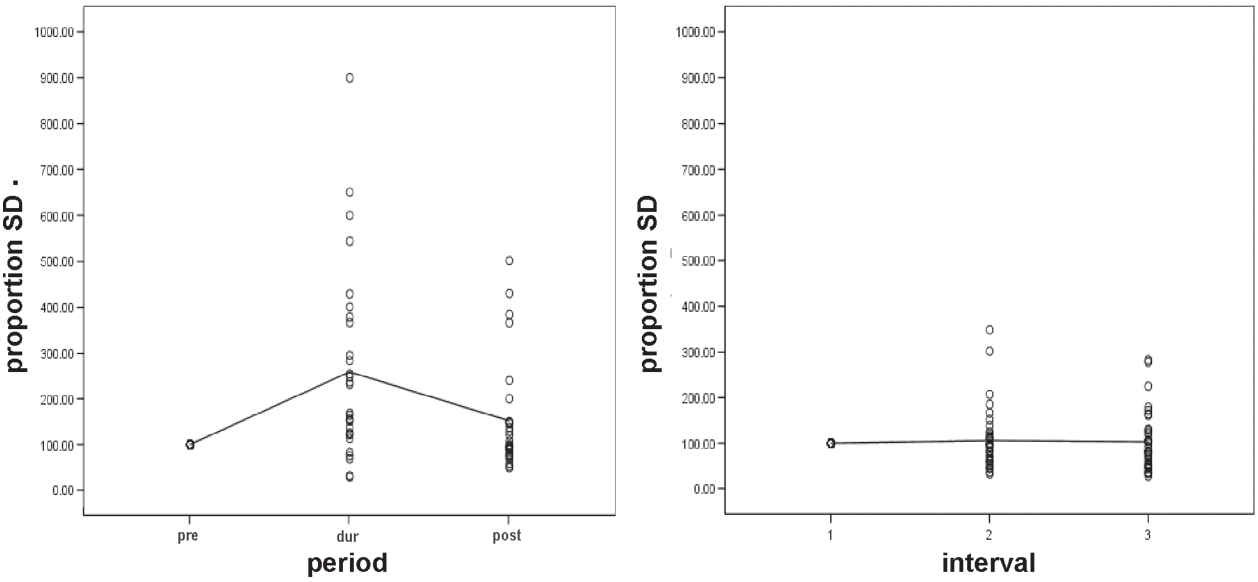

Figure 5.3.2-8 g: Proportional Changes in Standard Deviation Values of Heart Rate during Visit (left) and 'Baseline' (right) Sessions. Pre-visit values and values obtained for 1^{st} 'baseline'-intervals have been set to 100 %, values for the following periods/ intervals are expressed as changes from 100 %. Dots represent proportional values for single sessions; line: interpolation line.

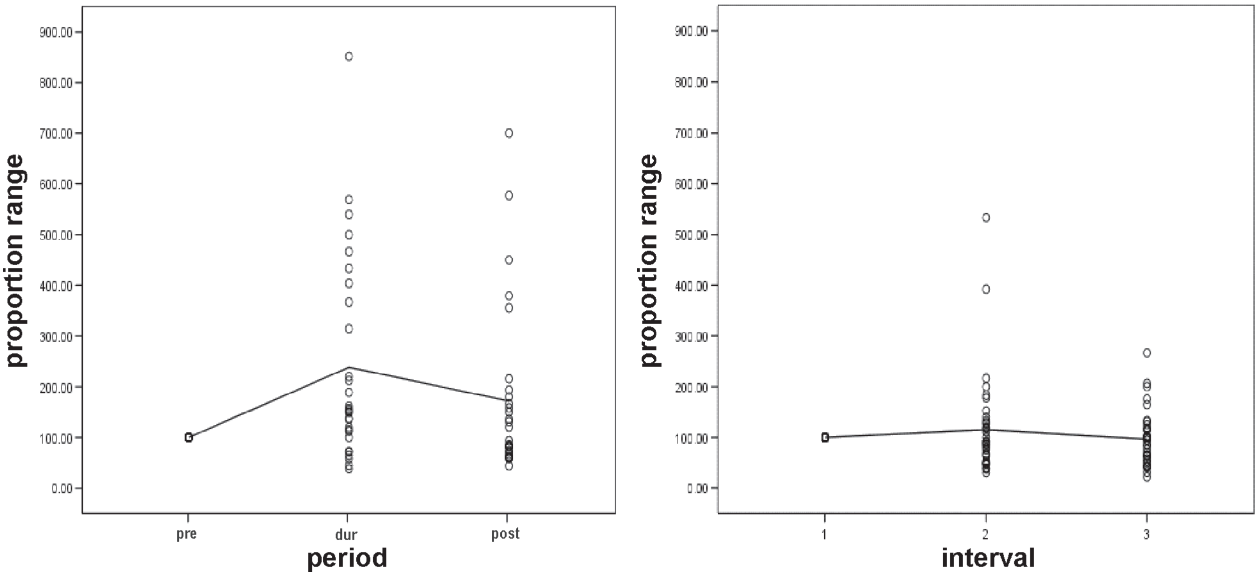

Figure 5.3.2-8 h: Proportional Changes in Range Values of Heart Rate during Visit (left) and 'Baseline' (right) Sessions. Pre-visit values and values obtained for 1^{st} 'baseline'-intervals have been set to 100 %, values for the following periods/ intervals are expressed as changes from 100 %. Dots represent proportional values for single sessions; line: interpolation line.

Tables 5.3.2-19 and 5.3.2-20 summarise the visual information provided by the scatterplots, comparing **during-visit** values with those of the **2nd ’baseline’-interval** (tab. 5.3.2-19), and **post-visit** values with those of the **3rd ’baseline’-interval** (tab. 5.3.2-20), respectively. Proportions of pre-visit/ 1st ’baseline’-interval values were categorised into 10 %-classes of which one class (green) contained the 100 % value at its ‘centre’.

Both tables (tabs. 5.3.2-19, 5.3.2-20) show that – with the exception of SD and range (see ‘brief postscript’ below) – *‘visited’* sessions in general deviated more pronouncedly (reaching classes further away from 100 %) than *‘baseline’* sessions from the values obtained during the pre-visit period/ 1st ’baseline’-interval. Moreover, the difference was due to categories above 100 %-pre-visit, i.e. increases in heart rate, while the magnitude of deviations below pre-visit values was similar to that found in *‘baseline’* sessions.

Table 5.3.2-19: Comparison of During-Visit Heart Rate Statistical Parameters with those Obtained in the 2nd 10 min-Interval in ‘Baseline’ Sessions. Figures represent number of sessions falling into each proportional category; e.g., 65-74: class contains values from 64.50 to 74.49; o: empty category; n (sess): total number of sessions. Colour code: **green**: ‘around’ 100 %, **grey**: more than 1 session in a category lower than 100 %, **orange**: more than 1 session in a category higher than 100 %. **N.b.:** Due to erratic distribution, SD and range remained uncoded. **bold** figures: ‘extreme’ classes for SD and range (not reached by other parameters); %pre-visit: during-visit value expressed as a proportion of pre-visit value (> 100 %: higher than pre-visit, < 100 %: lower than pre-visit); %1st interval: ditto; SD: standard deviation, Q 1: 1st quartile, min: minimum, max: maximum, Q 3: 3rd quartile.

during-visit n (sessions): 29									**2nd 'baseline'-interval n (sessions): 37**								
%pre-visit	**mean**	**SD**	**Q 1**	**min**	**median**	**max**	**Q 3**	**range**	**%1st int**	**mean**	**SD**	**Q 1**	**min**	**median**	**max**	**Q 3**	**range**
>204	o	**14**	o	o	o	o	o	**11**	>204	o	**3**	o	o	o	o	o	**3**
195-204	1	o	1	1	1	o	1	o	195-204	o	o	o	o	o	o	o	1
185-194	o	o	o	o	o	o	o	1	185-194	o	1	o	o	o	o	o	o
175-184	o	o	o	o	o	1	o	o	175-184	o	o	o	o	o	o	o	2
165-174	o	1	o	o	o	3	1	o	165-174	o	1	o	o	o	o	o	o
155-164	o	2	o	o	o	o	1	2	155-164	o	o	o	o	o	o	o	o
145-154	2	2	o	o	2	1	o	3	145-154	o	1	o	o	o	o	o	o
135-144	o	1	o	o	o	2	1	2	135-144	o	o	o	o	o	1	o	1
125-134	1	1	3	1	1	1	3	o	125-134	o	1	o	o	o	o	o	3
115-124	4	2	1	4	2	3	o	2	115-124	3	2	3	4	3	2	2	3
105-114	7	1	2	4	8	11	7	1	105-114	3	4	3	3	3	7	4	1
95-104	9	o	17	12	10	4	10	1	95-104	27	6	25	25	25	14	24	1
85-94	4	o	4	5	4	2	4	o	85-94	3	2	5	5	5	8	6	6
75-84	o	2	1	2	o	o	o	o	75-84	1	3	1	o	1	5	1	3
65-74	1	1	o	o	1	1	1	3	65-74	o	3	o	o	o	o	o	2
<65	o	**2**	o	o	o	o	o	**3**	<65	o	**10**	o	o	o	o	o	**11**

Particularly with respect to categories above 100 %, magnitudes of difference from pre-visit values as well as 1st ’baseline’-interval values were less pronounced in the **post-visit period** and **3rd ’baseline’-interval**, respectively, than they had been during-visitation/ in the 2nd ’baseline’-interval (tab. 5.3.2-20). As reductions were found regardless of visitation/ no visitation, however, the difference in magnitudes between *‘visited’* and *‘baseline’* sessions was not cancelled out.

Table 5.3.2-20: Comparison of Post-Visit Heart Rate Statistical Parameters with those Obtained in the 3rd 10 min-Interval in 'Baseline' Sessions. Figures represent number of sessions falling into each proportional category; e.g., 65-74: class contains values from 64.50 to 74.49; o: empty category. n (sess): total number of sessions Colour code: **green**: 'around' 100 %, **grey**: more than 1 session in a category lower than 100 %, **orange**: more than 1 session in a category higher than 100 %. **N.b.:** Due to erratic distribution, SD and range remained uncoded. **bold** figures: 'extreme' classes for SD and range (not reached by other parameters); %pre-visit: post-visit value expressed as a proportion of pre-visit value (> 100 %: higher than pre-visit, < 100 %: lower than pre-visit); %1st interval: ditto; SD: standard deviation, Q 1: 1st quartile, min: minimum, max: maximum, Q 3: 3rd quartile.

post-visit n (sessions): 29									3rd 'baseline'-interval n (sessions): 34								
%pre-visit	mean	SD	Q 1	min	median	max	Q 3	range	%1st int	mean	SD	Q 1	min	median	max	Q 3	range
>204	o	**5**	o	o	o	o	o	**6**	>204	o	**3**	o	o	o	o	o	**2**
195-204	o	1	o	o	o	o	o	o	195-204	o	o	o	o	o	o	o	1
185-194	o	o	o	1	o	o	o	1	185-194	o	o	o	o	o	o	o	o
175-184	o	o	1	o	o	o	o	1	175-184	o	1	o	o	o	o	o	1
165-174	1	o	o	o	1	1	1	1	165-174	o	1	o	o	o	o	o	1
155-164	o	o	o	o	o	o	o	1	155-164	o	1	o	o	o	o	o	o
145-154	o	4	o	o	o	o	o	1	145-154	o	o	o	o	o	o	o	o
135-144	o	1	o	o	o	2	o	1	135-144	o	o	o	o	o	1	1	o
125-134	o	1	o	1	o	3	o	1	125-134	1	2	1	1	1	o	o	2
115-124	5	1	4	3	3	1	5	1	115-124	o	2	o	o	o	1	1	2
105-114	6	1	7	7	8	7	6	o	105-114	2	3	3	5	2	6	2	1
95-104	9	3	10	8	9	6	9	o	95-104	19	2	19	21	22	10	18	7
85-94	7	4	7	7	7	8	7	2	85-94	11	1	10	7	8	10	10	1
75-84	1	3	o	2	o	1	1	4	75-84	1	5	1	o	1	6	2	2
65-74	o	2	o	o	1	o	o	3	65-74	o	2	o	o	o	o	o	2
<65	o	**3**	o	o	o	o	o	**6**	<65	o	**11**	o	o	o	o	o	**12**

■ A Brief Postscript: Focusing on Standard Deviation and Range

With standard deviation and range in themselves constituting measures of extent of variability in a given dataset, it was not surprising that, for both *'visited'* and *'baseline'* sessions, they were the least 'centred' of all parameters analysed (tab. 5.3.2-19 and tab. 5.3.2-20). Upon closer examination, however, their 'scattering' exhibited distinct patterns, particularly with respect to 'extreme' classes (< 65 %, > 204 %).

In the following passage, numbers of sessions which reached categories above/ within/ below the pre-visit/ 1st 'baseline'-interval values have been summed up.

During-visitation (tab. 5.3.2-19), standard deviation values of the greatest number of sessions were higher than pre-visit values (**24**: **0**: **5**). In approximately half of all sessions analysed, the difference was above 204 % (14 sessions > 204 %), while values below 65 % were calculated for only 2 sessions (2 sessions < 65 %). The same pattern was found for the parameter 'range' (**22**: **1**: **6**; 11 sessions > 204 %, 3 sessions < 65 %).

In contrast, in approximately half of all *'baseline'* (tab. 5.3.2-20) sessions, standard deviation values of the **2nd interval** were lower than values calculated for the 1st interval (**13**: **6**: **18**). Of these, more than a quarter of all sessions (10 of 37) were found in the category 'below 65 %', whereas only 3 sessions fell into the category 'above 204 %' (3 > 204 %, 10 < 65 %). Additionally, standard deviations of 6 sessions were very close to values calculated for the 1st 'baseline'-interval. A similar pattern – excepting the 'near-centre' values – was found for the parameter 'range' (**14**: **1**: **22**; 3 sessions > 204 %, 11 sessions < 65 %).

Post-visit (tab. 5.3.2-20), standard deviation values of an approximately equal number of sessions (**14**: **3**: 12) deviated above and below 100 %. Additionally, the category 'above 204 %' held considerably fewer sessions (than during-visit: 14 > 204 %), while little change was observed for the category 'below 65 %' (5 > 204 %, 3 < 65%) which had held 2 sessions during-visitation. **Compared to findings during visitation**, between-period change thus consisted mainly of a reduction in standard deviation values (fewer of the higher categories occupied), with values for 3 sessions falling into the category including 100 % (95 %-104 %), which had been unoccupied during visitation. A similar 'equalising' – again, excepting the 'near-centre' values – was found for post-visit range values (**14**: **0**: 15; 6 sessions > 204 %, 6 sessions < 65%)

With respect to the **3rd interval** of *'baseline'* sessions (tab. 5.3.2-20), standard deviation as well as range values exhibited **little difference to** the pattern described for the **2nd interval** (SD: **13**: **2**: 19; 3 sessions > 204 %, 11 sessions < 65 %; range: **10**: **7**: 17; 2 sessions > 204, 12 sessions < 65 %). Additionally, more than a fifth (7 of 34) of the range values fell into the category including 100 %.

Differences between *'visited'* and *'baseline'* sessions could thus even be found in the 'most variable' of all parameters examined. They were most notable during direct stimulus application (during visitation vs. 2nd 'baseline'-interval), but remained distinct even after stimulus removal (post-visit vs. 3rd 'baseline'-interval).

5.3.2.3 Section Summary

N.b.: This section summary will not dwell on regime differences, as these will be presented comprehensively for all sections together at the end of chapter 5.3.

Quantitative comparison of prevalence was undertaken for a total of **7 parameters**. For each of 6 behaviours (resting, comfort, breeding, vigilance, agonistics, headshakes) and the posture 'prone', proportions of time allocated to each parameter were calculated pre-, during-, and post-visit, and the periods were subsequently compared.

With respect to **heart rate**, heart rate variation was analysed using a total of **8 statistical parameters** (mean, median, minimum, maximum, 1st quartile, 3rd quartile, SD, and range). Analyses were effected for **'visited'** as well as **'baseline' sessions** (no human interference). Variation in these parameters was compared across periods (pre-, during-, and post-visit; 'visited' sessions), across successive 10 min-intervals (1st, 2nd, and 3rd; 'baseline' sessions), and subsequently, between 'visited' and 'baseline' sessions.

For all behaviours examined as well as for posture, proportions only rarely returned to pre-visit levels; instead, incomplete **recovery** or 'overshooting' were frequently observed.

With respect to **magnitude of differences** in responses between pre- and post-visit found in individual sessions, the range of between-period values (span from min. to max.) was substantial for all parameters, pointing to the **persisting individuality** of behavioural and postural post-stimulus responses and, ultimately, recovery.

Despite a pervading tendency towards individuality, the following overall results may be stated: **During human visitation**, behaviour (particularly the behaviour systems of resting, vigilance, as well as headshakes), posture ('prone'), and a number of heart rate statistical parameters (particularly maximum, range, and standard deviation) were significantly different from pre-visitation levels (**direction of change**).

After visitation, the cessation of human presence did not generally result in complete recuperation in the post-visit period.

As regards heart rate statistical parameters, a **comparison of 'visited' and 'baseline' sessions** (sessions without human visitation) showed that increases found during visitation were not paralleled by increases in the corresponding 2nd 'baseline'-interval. While deviations from initial values (obtained in the pre-visit period/ 1st 'baseline'-interval) were found in both types of sessions, the **magnitude** of increases was generally greater for '*visited*' than for '*baseline*' sessions, while the magnitude of decreases was similar for both types.

5.3.3 Distribution of Behaviour and Heart Rate Phases and Posture States

After the analysis of between-period (before, during, and after human visitation) differences in prevalence of behaviour systems and posture as well as extent of heart rate variation (key question: How much?), this section focuses on between-period differences in **phases** (behaviour and heart rate) and **states** (= posture 'phases') to examine whether the distribution of phases/ states observed prior to visitation changed in frequency (phase/ state number) and/or duration (phase/ state time) during and after human visitation. Alterations in 'flow' are examined by quantifying changes in distribution (i.e. changes in number of distinct phases/ states, and the time these take up).

Recapitulation: In this context, **'flow'** combines the overall presence of behaviours belonging to a given **behaviour system** with the duration of **phases** found within that system as well as capturing changes between different behaviour systems (e.g., comfort 2 min, vigilance 20 s, comfort 10 s, vigilance 5 s) and 'smoothness' of **transitions** between systems (e.g., instant switches between systems, interruptions of one system by elements pertaining to another system, transitionary phases comprising elements of two different systems).

Taken together, these are referred to as the focal animal's behavioural rate **topography** (and, analogously examined, postural and heart rate topography).

Between-period comparison in this section looks for **structural and compositional changes in topography** to examine just how the animals alter their behaviour to arrive at the changes in prevalence of behaviour systems and specific postures and the extent of heart rate variation found in the previous section.

The term 'structural alterations' refers to changes in the **'syntax'** of comportment which may concern all categories (e.g., more and overall shorter behaviour phases) or specific categories (e.g., more and longer states of posture 'up'). Depending on interplay of number and time of phases/ states, structural alterations will or will not cause changes in the **composition** of comportment (i.e., more resting phases need not result in more time spent resting, if long resting phases disappear and short resting phases do not increase dramatically).

The key question in this section thus asks **'In what way?'**

Results are at first presented for ***all regimes***; following, ***regime differences*** are illustrated for selected categories.

5.3.3.1 Methodological Prelude

5.3.3.1.1 Secondary Transcriptions of Focal-Animal Comportment and Disturbance

Secondary transcriptions focused on between-period differences in distribution (phase/ state duration and number) of each of the behaviour systems, both postures, and heart rate in relation to human disturbance. The Visiting Stage Performance Indicator Value (q.v.; tab. 5.3.1-3) served to distinguish the period of **human visitation** from periods before and after the visit. **Conspecific** and **predator/ aircraft** disturbance do not feature in this section.

■ Behaviour Phases

Definition: To achieve a quantitative measure of changes in flow, behaviour elements pertaining to the same behaviour system were grouped into behaviour phases. For the purpose of this thesis, the definitions presented in box 5.3.3-1 were employed. Definitions provided starting and end-points, and categorised phases according to ‘ingredients’ (e.g., ‘pure’, transitionary, interruption). Behaviour phases had a minimum duration of 3 s; maximum possible duration was limited only by recording time.

Box 5.3.3-1: Definitions Used in the Analysis of Behaviour Phases. A, B, C, D, E, F: different behaviour systems; [B(B)]: 1 or 2 s of behaviour system B within a phase from another behaviour system (A), [BD]: 2 s (one each of behaviour systems B and D) within a phase from yet another behaviour system (C).

Definitions and Examples – Behaviour Phases

Pure phase (minimum 3 s): behaviour elements from one behaviour system

AAA

CCCCCCCCCCCCCCCCC

Impure phase (minimum 7 s, minimum 3 s on either side of ‘impurity’, s.b.**):** phase containing spurious elements from (an)other behaviour system(s)

AAA [B(B)] AAA, with [] = impurity

CCC [BD] CCC, with [] = impurity

Also see box 5.3.3-2

Transitionary phase (minimum 3 s): a particular type of interruption (s.b.); in-between phases of two different behaviour systems; behaviour elements from the two behaviour systems, changing every one or two seconds

AAA [CAACACCAACCA] CCC, with [] = transitionary phase

Interruption s.s. (minimum 3 s): behaviour elements from a minimum of two different behaviour systems, changing every one or two seconds; either flanked by the same behaviour system on both sides (‘within-phase interruptions’) or separating different behaviour systems (‘between-phase interruptions’); interruptions end once behaviour from the same system has been shown for at least 3 s

CCC [DAACCDDEFDDABAAFB] AAA, with [] = between-phase interruption

Interruptions s.l.: Although interruptions were originally transcribed separately as ‘within-phase interruptions’, ‘between-phase interruptions’, and ‘transitionary phases’, they were analysed collectively: ‘interruptions s.l.’. This category also included the extremely rare occurrences of ‘headshake phases’ (headshakes in 3 consecutive seconds).

Interruptions s.l. constituted an additional parameter (alongside phases pertaining to a single behaviour system) for which changes during disturbance were investigated.

‘Impurity’ (maximum 2 s): spurious elements from one behaviour system within a phase from another behaviour system (‘within-phase impurity‘) or in-between phases from two different behaviour systems (‘before-phase impurity’; for examples, also see impure phase)

N.b.: If two behaviour systems occurred within the same second, the behaviour shown in the first half of the second was counted.

Condensation: Prior to determination of phase durations, the behaviour record was condensed (see box 5.3.3-2). Using second-by-second transcriptions of focal-animal behaviour, all **single seconds of resting behaviour** were counted with the behaviour system that followed (step 1).

Following that (step 2), **'within-phase impurities '** (one or two seconds of behavioural elements of one behaviour system enclosed by phases of a second behaviour system on both sides) were counted through and noted as part of that phase. Likewise, **'before-phase impurities'** (one or two seconds of behavioural elements of one behaviour system in-between two phases from a second and third behaviour system) were counted with the following system and noted as part of that phase. After this (step 3), **interruptions s.s.** and **transitionary phases** were identified.

Additionally, the **extent of impurity** was expressed as proportion of entire phase duration: The greater the number of elements not pertaining to that behaviour system, the greater the proportion of impurity of a given phase.

N.b.: Headshakes (including head- as well as ruffle-shakes) and **displays** do not figure as phases in their own right due to their brevity (majority of headshakes) or rarity of occurrence (long bouts of shaking, particularly displays, which were only observed prior to visitation). Headshakes, however, were a common element of interruptions (s.a.) within or between phases. Similarly, the comportment parameter **'scattering'** is to some extent retrieved in 'interruptions'.

Box 5.3.3-2: Rules employed to 'Condense' Behaviour. A, B, C, D, E, F: different behaviour systems; (A)A: 1 s or 2 s of behaviour system A. <u>R</u>: single second of resting behaviour

Rules for 'Condensation' of Behaviour

re step 1: Single seconds of resting behaviour were counted with the following system <u>before</u> further condensation occurred:

AAA **BAC<u>R</u>** CCC ➔ AAA BA CC CCC ➔ AAA CC CC CCC

re step 2: Phases (minimum 3 s); were at times interspersed with **'impurities'** (but then needed a minimum of 3 s on either side of it); impurities were integrated as follows:

AAA **B(B)** AAA ➔ B → A (one long phase)

AAA **B(B)** CCC ➔ B → C (phase C is extended)

DEF **BB** CCC ➔ B → C (phase C is extended)

AAA **B(B)** DEF ➔ B → DEF (interruption is extended)

re step 3: Interruptions s.l. (minimum 3 s; separate phases of same or different behaviour system(s) were dealt with as follows:

AAA **BA(A)B** AAA ➔ 'within-phase-interruption' (two phases of same behaviour system)

AAA **DEF** AAA ➔ 'within-phase-interruption'

AAA **BCB** CCC ➔ 'between-phase-interruption' (two phases of different behaviour systems)

AAA **BACB** CCC ➔ 'between-phase-interruption'

DEF **B(B)** DEF ➔ one long interruption

Overlaps: Phases lasting across period boundaries were accommodated as follows:

The entire phase was assigned to the period **within which its greater proportion had occurred**. In case of **ties** (equal proportions in both periods), the phase was assigned to the period it had started in. While obscuring actual recording times per period, these results represent **correct phase durations** and avoid artificial increase of phase **frequencies** (result of splitting).

Duration Classes: Phase durations were assigned to three *duration classes*, each of which was divided into three *subclasses* (table 5.3.3-1). Class and subclass ranges were chosen within the min.-max. distributions observed across all sessions.

Table 5.3.3-1: Classes and Subclasses of Phase Duration – Behaviour. n.a.: not applicable.

Duration Class	Range of Phase Duration in Subclasses	Gain onto Previous Subclass
short: 03 - 30 s	03 s to 10 s	n.a.
	11 s to 20 s	+10 s
	21 s to 30 s	+10 s
medium: 31 - 120 s	31 s to 60 s	+30 s
	61 s to 90 s	+30 s
	91 s to 120 s	+30 s
long: 121 - >240 s	121 s to 180 s	+60 s
	181 s to 240 s	+60 s
	>240 s	+whatever

■ Posture States

Definition: Posture was classified as either ‘prone’ or ‘up’ (the latter combining sitting and standing postures). Posture states were **defined** as constituting lengths of time spent in a given category (‘prone’, ‘up’).

A given state ended as soon as a posture change occurred. Posture states lasted from 1 s (e.g., ‘up’: briefly ‘lunging’ towards a conspecific to avoid nest stone theft; ‘prone’: trying to lie down upon as yet unsuccessfully arranged eggs) up to the duration of the entire record (only observed for posture ‘prone’). Unlike in behaviour phases, changes in posture state remained uncondensed (e.g., 1 s of ‘up’ was not ‘counted through’).

Overlaps: States lasting across boundaries between two or even all three periods, were common, and regularly reached far into the following period(s). Rather than trying to assign them to any one period – and losing the better part of the other –, these were included for analysis of **change rates** only, but did **not** feature in analyses of **state durations**.

Duration Classes: For postures, state durations were likewise assigned to three *duration classes*, each of which was divided into three *subclasses* (table 5.3.3-2). Class and subclass ranges were chosen within the min.-max. distributions[1] observed across all sessions. Due to their greater range, class borders differ from those chosen for behaviour phases.

■ Heart Rate Phases

Determination of Mean Resting Heart Rate: In each heart rate record, between 3 and 10 pre-visit 20 s-values of heart rate obtained during the behaviour system of resting (number of values according to availability) were used to determine **mean resting heart rate** (RHR) and its standard deviation (SD). Values were considered only, if the 20 s-interval for which the heart rate value had been calculated contained a minimum of 15 s ‘at rest’; additionally, resting behaviour had to have been displayed for a minimum of 10 s in the previous 20 s-interval.

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[1] disregarding durations longer than entire periods

Table 5.3.3-2: Classes and Subclasses of State Duration – Posture. n.a.: not applicable.

Duration Class	Range of State Duration in Subclasses	Gain onto Previous Subclass
short: 01 - 60 s	01 s to 10 s	n.a.
	11 s to 30 s	+20 s
	31 s to 60 s	+30 s
medium: 61 - 240 s	61 s to 120 s	+60 s
	121 s to 180 s	+60 s
	181 s to 240 s	+60 s
long: 241 - >480 s	241 s to 360 s	+120 s
	361 s to 480 s	+120 s
	>480 s	+whatever

Following Neebe & Hüppop (1994; also see Ellenberg & al. 2006), **mean RHR ±2 SD** was then taken as a tolerance band for the remainder of the heart rate record during a given session. Calculations resulted in **three heart rate categories** used for further analyses: below RHR ±2 SD, within RHR ±2 SD, and above RHR ±2 SD.

Definition: Analogous to the different behaviour systems, heart rate phases thus constituted lengths of time spent in a given category. As heart rate data consisted of counts per 20 s, and the resulting number of beats was used to assign any given 20 s-interval to a category, **phase durations** invariably lasted (multiples of) 20 s.

Overlaps: Phases extending across period boundaries were accommodated as described with respect to behaviour systems: The entire phase was assigned to the period **within which its greater proportion had occurred**. In case of **ties** (equal proportions in both periods), the phase was assigned to the period it had started in. While obscuring actual recording times per period, these results represent **correct** phase **durations** as well as phase **frequencies**.

Duration Classes: For heart rate, phase durations were likewise assigned to three *duration classes*, each of which was divided into three *subclasses*. Class and subclass ranges were chosen within the min.-max. distributions observed across all sessions. Accommodating 20 s-intervals and a greater range (than behaviour phases), the following classes resulted (tab. 5.3.3-3).

Table 5.3.3-3: Classes and Subclasses of Phase Duration – Heart Rate. Heart rate phases invariably lasted (multiples of) 20 s, as values counted for 20 s-intervals served to assign the respective intervals to one of three heart rate categories, viz., ‘below’, ‘within’, and ‘above’ resting heart rate ±2 SD. n.a.: not applicable.

Duration Class	Range of Phase Duration in Subclasses	Gain onto Previous Subclass
short: 20 - 60 s	20 s	n.a.
	40 s	+20 s
	60 s	+20 s
medium: 80 - 240 s	80 s to 120 s	+60 s
	140 s to 180 s	+60 s
	200 s to 240 s	+60 s
long: 260 - >480 s	260 s to 360 s	+120 s
	380 s to 480 s	+120 s
	>480 s	+whatever

5.3.3.1.2 Presentation of Results

Comparison of between-period changes: The duration of phases (behaviour and heart rate categories)/ states (posture categories) was examined for each period (pre-visit, during-visit, post-visit). Two aspects were analysed:

- Number of phases/ states of each duration subclass
- Amount of time taken up by phases/ states of each duration subclass

With respect to behaviour phases, numbers and durations of 'impurities' (behavioural elements not belonging to the behaviour system of the phase) which were counted through were additionally noted (as a proportion of the phase they pertained to).

For comparison of distributions of observed **phase/ state durations** across behaviour systems/ between posture states/ across heart rate categories as well as across periods, **proportions** were calculated:

- Proportion of ***total phase/ state number***: The total number of phases/ states (for which durations had been obtained) observed for all parameters (i.e., all behaviour/ posture/ heart rate categories) within a given period, constituted 100 %. This way, it was possible to compare relative distributions <u>between categories</u> within a period without losing sight of their relative distributions across periods.
- Proportion of ***category phase/ state number***: The number of phases/ states observed for each category within a given period, constituted 100 %. This aided comparisons of <u>within-category</u> changes (between periods) for each parameter (each behaviour/ posture/ heart rate category) examined. (Proportional category phase/ state numbers were added to figures for values of 5 % and above).
- Proportion of ***total phase/ state time***: The total time (in seconds) of phases/ states of known duration observed for all categories within a given period, constituted 100 %. This way, it was possible to compare relative distributions <u>between categories</u> within a period without losing sight of their relative distributions across periods.
- Proportion of ***category phase/ state time***: The total time (in seconds) of phases/ states of known duration observed for each category within a given period, constituted 100 %. This aided comparisons of <u>within-category</u> changes (between periods) for each parameter (each behaviour category/ posture category/ heart rate category) examined. (Proportional category phase/ state times were added to figures for values of 5 % and above).

Order of Presentation: With respect to between-period changes for all regimes together, the same **order of presentation** has been adopted for <u>behaviour</u>, <u>posture</u>, and <u>heart rate</u>, respectively:

1. <u>Total phase/ state number and time</u> for <u>all</u> categories and <u>individual</u> duration subclasses (*allCats-indScls*): To examine **changes in overall flow** (e.g., a general reduction/ prolongation of phase/ state duration irrespective of category) results are presented for all categories together assigned to the individual durations subclasses (figs.: pie charts) depicting total phase/ state number (numbers of phases/ states of known duration in each period) and total phase/ state time (time in seconds allotted to all phases/ states of known duration in each period).
2. <u>Total phase/ state number and time</u> for <u>individual</u> categories and <u>all</u> duration subclasses (*indCats-allScls*): To briefly illustrate **between-category changes** with respect to phases (e.g., more phases of 'rest', less phases of 'vigilance'), results on individual categories irrespective of

duration subclass are shown (figs.: log-diagrams; first log). Within each category, results are again listed for proportions of total phase/ state number and time.

3. Category phase/ state number and time for individual categories and individual duration subclasses (*indCats-indScls*): To examine **within-category changes** (e.g., more short phases of ‘rest’), results on individual duration subclasses of individual categories are provided within the same log-diagrams (in figs.: subsequent logs) for category phase/ state number and time.

Comparison of regimes will be presented as follows: For the five categories examined per regime (‘rest’, ‘vigilance’, ‘interruptions s.l.’, ‘heart rate_within’, ‘heart rate_above’), **ranked magnitudes of response** are jointly presented (tabs. 5.3.3-8a, -9a, -10a, and tabs. 5.3.3-8b, -9b, -10b). They provide an overview of increases/ decreases in total phase number and time (all phases pertaining to that category per period, expressed as a proportion of all phases per period) by presenting pair-wise differences (i.e., between-period changes from pre- to during-visitation, from during- to post-visitation, and from pre- to post-visitation).

To enable gauging the impact of the changes, proportions of total phase number and time calculated for the referential period (i.e., for changes from pre- to during-visitation: pre-visit proportions, from during- to post-visitation: during-visit proportions) have been place in the middle of each table; decreases are depicted left of referential proportions, and increases are shown right of referential proportions. Rank -4 was assigned to the most pronounced decrease, while the most pronounced increase received rank +4. Ranks were filled in from greatest to smallest magnitudes (from ±4 to ±1). As for ties, the ‘higher’ rank was awarded to both/ all concerned, and the following rank position(s) remained ‘unoccupied’. Changes smaller ± 1 % have been excluded from rankings.

Recapitulation: The difference between **pre- and during**-visit proportions is considered to reflect the immediate effect of visitation, while the difference between **during- and post**-visit proportions is suggested to shed light on the focal animals’ continuing/ waning response after withdrawal of the stimulus. The difference between **pre- and post**-visit proportions thus gives an indication as to the extent to which the animals have managed or failed to achieve recovery during the post-visit period.

Log-Diagrams: Log-diagrams are based on results for all regimes together. Within each figure (pre-, during-, and post-visitation, resp.), they depict **total phase/ state** (*indCats-allScls*) for both **number** (left-hand, from top to bottom) and **time** (right hand) in the first (‘bricked’) logs. The subsequent logs display **category phase/ state number** and **time** (*indCats-indScls*).

Total phase/ state number and time (*indCats-allScls*): Within a given period, total number/ time of phases (behaviour, heart rate) or states (posture) observed for all categories constitutes 100 % (e.g., pre-: all resting phases + all comfort phases + … + all interruptions s.l. = 100 %). This way, it is possible to compare relative distributions between categories within a period without losing sight of their relative distributions across periods. These proportions are displayed on the Y-axes and are depicted in the first (‘bricked’) log in each figure.

Category phase/ state number and time (*indCats-indScls*): To highlight changes found within each behaviour/ posture/ heart rate category, logs representing the different duration-subclasses (subsequent logs) have been additionally supplied with labels denoting within-category proportions for which all durations within a given behaviour/ posture/ heart rate category constitute 100 % (e.g., pre-: all resting phases in subclass 1 + all resting phases in subclass 2 + … + all resting phases in subclass 9 = 100 %) for values of 5% or higher. As decimals have been rounded off in the figures (5 % instead of 4.67 %), the reader will find the occasional **incongruence** between proportional values presented in the figure and between-period or class values reported in the text.

N.b.: While **figures** depict all nine **subclasses**, the **text** will mainly refer to **classes**. Exceptions are made when distinguishing the subclass in which the greatest proportion of phase number/ time was found and when describing behaviour categories which predominantly/ exclusively 'occupied' only one class, e.g., 'interruptions s.l.'.

5.3.3.2 Between-Period Changes – All Regimes

Data presented in this section are based on 50 sessions (behaviour phases), 51 sessions (posture states), and 27 sessions (heart rate phases), respectively, to which individual focal animals contributed differently (tab.: 5.3.3-4).

Between-period changes were examined with respect to the behaviour categories 'rest', 'comfort', 'breed', 'vigilance', 'agonistic behaviour', and 'interruptions[2] s.l.', the posture categories 'prone' and 'up' as well as the heart rate categories 'below', 'within', and 'above' resting heart rate (RHR) ±2 SD.

Table 5.3.3-4: Database Used (Behaviour Phases, Posture States, and Heart Rate Phases) for Distribution of Phase/ State Durations. With respect to posture, first values give total number and time, and values in brackets represent within-period number and time after elimination of overlapping states. FA: focal animal; n(Sess.): number of sessions; n(FAs): number of FAs; pre-: prior to visitation, dur-: during human visitation, post-: after human visitation; TPN: total phase number, TStN: total state number, TPT: total phase time, TStT: total state time.

	Behaviour			Posture			Heart Rate		
n (Sess.)	50			51			27		
n (FAs)	19			19			12		
Phase/ State Number	4805			436[#] (351)			462		
TPN/ TStN per Period (pre-, dur-, post-)	1430	1541	1834	92	101	158	143	124	195
Phase/ State Time (s)	76689			86586 (24397)			37800		
TPT/ TStT per Period (s) (pre-, dur-, post-)	25833	23545	27311	6657	4378	13362	13920	10600	13280

[#] comprising 385 changes between the two posture states, and 51 states recorded at the end of sessions

As mentioned above, **figures** depict all nine **subclasses**, while the **text** mainly refers to **classes**, viz., short-, medium-, and long-durations classes.

Class proportions are **calculated** by summing up proportions for subclasses 1 to 3 (short-durations class), subclasses 4 to 6 (medium-durations class), and subclasses 7 to 9 (long-durations class), respectively. All class-values have been tabulated in appendix 5.3.3-1.02 to 5.3.3-1.04.

5.3.3.2.1 Total Phase Number and Total Phase Time for All Behaviour Categories

Summing up, results for all behaviour categories and individual duration subclasses (*allCats-indScls*) indicate a slight tendency towards decreases in phase duration (more phases of shorter duration which take up more of overall time) from **before- to during**-visitation as well as from **during- to post**-visitation (fig. 5.3.3-1a, -b). In the short-durations class, ***total phase number***

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[2] of which headshakes (incl. ruffle-shakes) are frequent components

increased by 2 % (during-visitation) and a further 1 % (post-visitation), respectively. This was paralleled by a 7 % plus 3 % increase in ***total phase time*** assigned to this class.

Time-wise, the complementary losses were more pronounced in the long-durations class, while phase number was more affected in the class comprising medium durations.

The fact that during visitation proportion of phase time for the long-durations class decreased by 6 % whereas proportion of phase number was reduced by only 1 % indicates within-class reductions in phase duration in addition to those extending across classes.

Following, results are presented in detail.

To examine changes in overall phase durations, proportions of total phase number and time before, during and after human visitation were compared for individual duration subclasses and all behaviour categories together (*allCats-indScls*; i.e., irrespective of category).

With respect to ***total phase number***, only slight changes became apparent (fig. 5.3.3-1a):

In **all periods**, the first duration subclass (03-10 s) contained the greatest proportion of all phases of known duration (63 % pre-visit, 64 % during-visit, and 66 % post-visit).

Pre-visit, 86 % of all phases of known duration fell into the short-durations class (3-30 s), 12 % were assigned to the class of medium durations (31-120 s), while the class of long durations (121- >240 s) accounted for 2 % of the phases examined.

During-visit as well as **post-visit**, proportions of phases sorted into the short-durations class increased slightly (to 88 %, and 89 %, resp.), while those for the medium-durations class decreased slightly (to 11 %, and 10 %, resp.). The long-durations class likewise decreased slightly (to 1 %) during visitation and remained at that level after visitation had ended.

Looking at ***total phase time*** (*allCats-indScls*; proportions of time taken up by the respective subclasses) **before** human visitation, the greatest proportion was assigned to the subclass 31-60 s (first subclass of medium duration: 20 %), while **during** as well as **after** visitation, the lowest duration subclass (03-10 s) accounted for the greatest proportion of time (21 %, and 24 %, resp.; fig. 5.3.3-1b).

Pre-visit, the short-durations class represented 41 % of total phase time; the medium-durations class held 39 %; and 20 % of total phase time were assigned to the class of long durations.

During-visit as well as **post-visit**, proportions of phase time accounted for by the short-durations class increased (to 48 %, and 51 %, resp.), while those of medium- (to 38 %, and 36 %, resp.) and long-durations classes (to 14 %, and 12 %, resp.) decreased.

5.3.3.2.2 Rest

Summing up, the overall proportion of phases of resting behaviour for all duration classes (*indCats-allScls*; in fig. 5.3.3-2a and b: ‘bricked’ logs) decreased (as compared to pre-visit) **during** visitation with respect to both total number of phases recorded and total time taken up by these phases. **After** visitation, proportions re-increased but failed to make a complete **recovery**.

Within the category ‘rest’, between-period changes in individual duration classes (*indCats-indScls*) were prominent (fig. 5.3.3-2a and b): **During** visitation, phases of short duration increased, both in number as well as time taken up, while phases of medium and long duration decreased. **After** visitation, a shift towards longer durations occurred, but did not effect a complete **recovery** (with

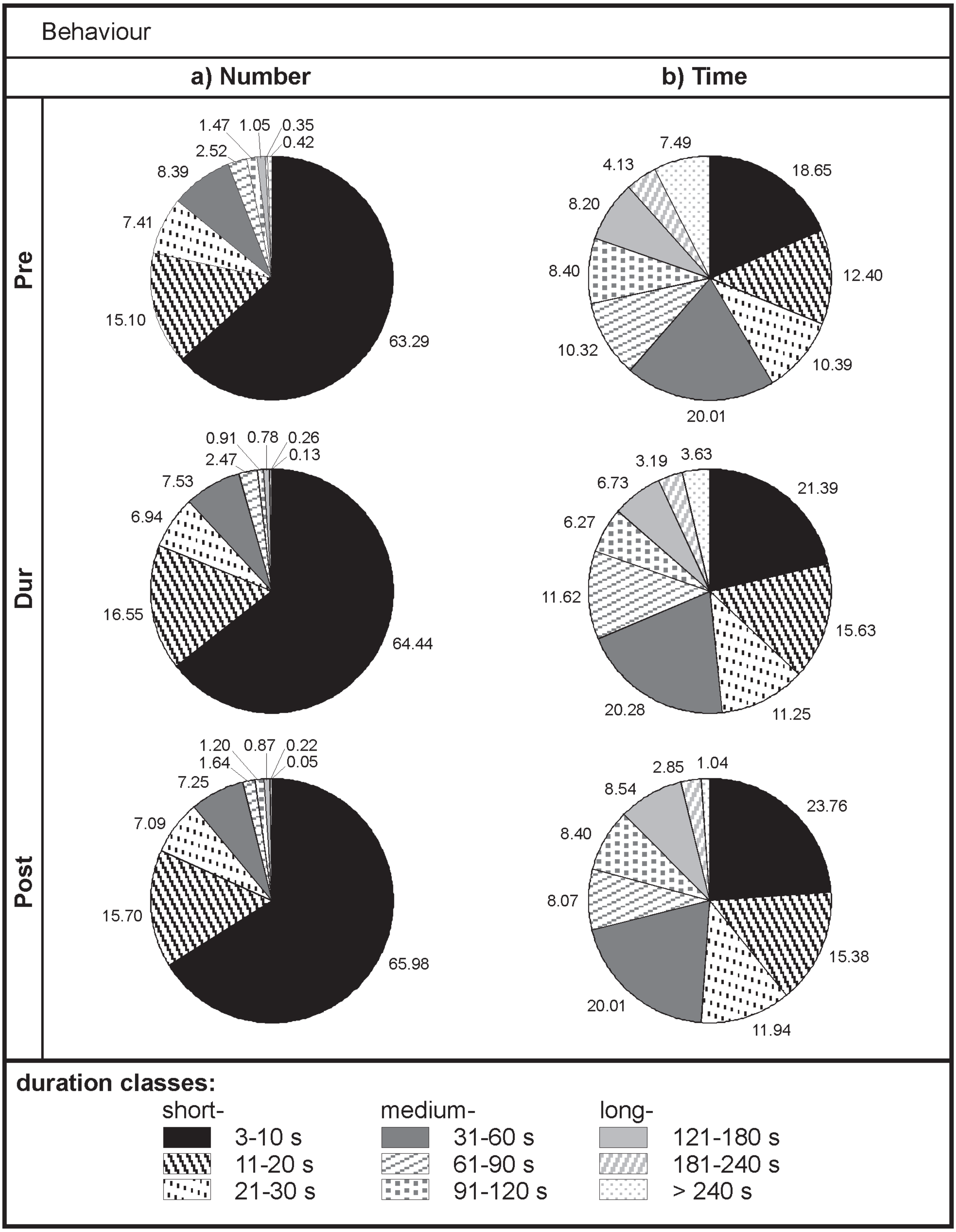

Figure 5.3.3-1a) and -b): Proportions of Duration Subclasses of a) Total Phase Number (left) and b) Total Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation for All Behaviour Categories Together (‘rest’, ‘comfort’, ‘breed’, ‘vigilance’, ‘agonistics’, ‘interruptions s.l.’). Number: total phase number, Time: total phase time; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 1430 phases, 25833 s; during-visit: 1541 phases, 23545 s; post-visit: 1834 phases, 27311 s.

the exception of phase time assigned to the medium-durations class). Phases exceeding 240 s were particularly affected.

The **overall amount** of resting behaviour was **reduced** after visitation; additionally, resting **phases** tended to be **shorter** in duration.

Following, results are presented in detail.

***Total Phase Number*: Before** human visitation, 36 % of the total phase number (*indCats-allScls*, 'bricked' logs) for all duration classes together were assigned to the behaviour system of 'rest' (fig. 5.3.3-2a). **During** visitation, the proportion dropped to 26 %. The re-increase **after** visitation (to 33 %) did not result in a complete **recovery**.

***Total Phase Time*: Before** human visitation, 62 % of the total phase time (*indCats-allScls*, 'bricked' logs in fig. 5.3.3-2b) for all duration classes together were assigned to the behaviour system of 'rest'. **During** visitation, the proportion dropped to 23 %. The re-increase **after** visitation (to 49 %) did not result in a complete **recovery**.

***Category Phase Number*:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-2a), the greatest proportion of resting phases of known duration was assigned to the subclass 03-10 s[3] in **all periods** (44 %, 65 %, and 55 %, resp.).

Pre-visit, 72 % of all resting phases fell into the short-durations class, 23 % were assigned to the class comprising medium durations, while the class of long durations held 5%. **During-visit** proportion of number of resting phases in the short-durations class increased by 18 % (to 90 %), while proportions for the medium- and long-durations classes decreased (to 9 %, and 1 %, resp.). **Post-visit**, there was a 10 % decrease in the short-durations class (to 80 %), accompanied by increases in medium- and long-durations classes (to 17 %, and 3 %, resp.).

In terms of **recovery** (comparing pre- to post-visit values), the short-durations class held 7[4] % more of all resting phases after visitation than prior to visitation, while classes of medium and long durations were reduced by 6 % and 2 %, respectively.

***Category Phase Time*:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-2b), phases assigned to the subclass 31-60 s[5] accounted for the greatest proportion of time **prior to** and **after** visitation (20 %, and 23 %, resp.), whereas equal proportions of time resulted from phases of the subclasses 03-10 s and 31-60 s **during** visitation (23 % each).

Pre-visit, resting phases in the short-durations class accounted for 25 % of the overall time spent resting, 44 % of that time was taken up by phases assigned to the medium-durations class, while 31 % of overall resting time resulted from phases of long durations. **During-visit** proportions of resting time of phases in the short-durations class increased by 31 % (to 56 %). This was accompanied by a decrease in proportions of resting time of phases assigned to the medium-durations class (-9 %, to 35 %) and, particularly, to the long-durations class (-22 %, to 9 %). **Post-visit**, there was a 23 % decrease in proportion of time of phases assigned to the short-durations class (to 33 %), accompanied by increases in proportions of time of phases sorted into medium- and long-durations classes (to 44 %, and 23 %, resp.). In terms of **recovery** (comparing pre- to

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[3] first subclass of the short-durations class

[4] doesn't tally due to rounding-off error; exact values:+7.387; -5.713; -1.674

[5] shortest of the medium-durations class

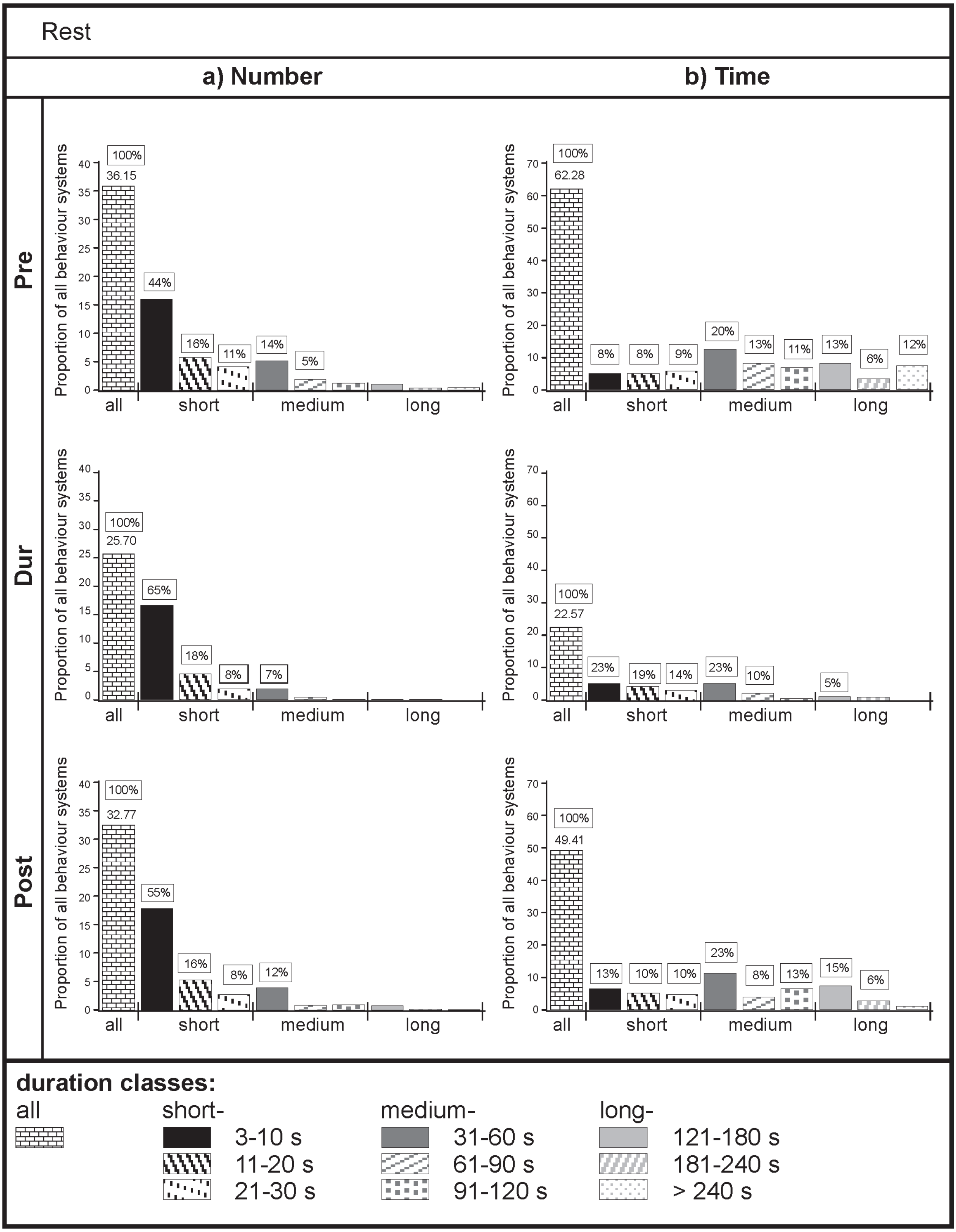

Figure 5.3.3-2 a) and b): Proportions of Duration Subclasses for the Behaviour Category <u>'rest'</u>: a) Phase Number (left) and b) Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first ('bricked') log show proportion of 'rest' with respect to <u>total</u> phase number and time (all phases from all categories = 100 %); %-values above logs represent proportions of <u>category</u> phase number and time (all phases of 'rest' = 100 %). Number: total phase number, Time: total phase time; all = all duration (sub-)classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 517 phases, 16090 s; during-visit: 396 phases, 5314s; post-visit: 601 phases, 13493 s. ['invisible' value for post-visit phase number, duration > 240 s = 0.17 %]

post-visit values), proportion of time of phases assigned to short-durations classes increased by 8 %, while proportion of time of phases sorted into the long-durations class decreased by the same amount. Within the long-durations class, the subclass of phases exceeding 240 s was particularly affected (decrease from 12 % to 2 %). No change in proportion of time (pre-visit vs. post-visit) was found with respect to the class comprising medium durations.

5.3.3.2.3 Comfort

Summing up, the overall proportion of phases of comfort behaviour for all duration classes (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-3a and b) exhibited a slight decrease (as compared to pre-visit) **during** visitation with respect to both number of phases recorded and time taken up by these phases. **After** visitation, proportions re-increased. While ***total phase number*** post-visit was approximately equal to the pre-visitation value, ***total phase time*** after visitation exceeded that found prior to visitation.

Within the category ‘comfort’, the following between-period changes in individual duration classes were found (*indCats-indScls*; fig. 5.3.3-3a and b): **During** visitation, phases of short duration increased, both in number as well as time taken up, while phases of medium duration decreased. **After** visitation, a within-class shift towards longer phases was evident, particularly in the short-durations class.

The **overall level** of comfort behaviour after visitation was approximately unchanged in terms of **numbers** but **augmented** in terms of **time** taken up; the remaining **phases** thus tended to be **longer** than prior to visitation.

Following, results are presented in detail.

***Total Phase Number*: Before** human visitation, 3 % of the total phase number of phases of known duration for all duration classes together (*indCats-allScls*) were assigned to the behaviour system of ‘comfort’. **During** visitation, the proportion dropped to 2 %. The re-increase **after** visitation (to 3 %) led to a complete **recovery** in terms of total phase number (‘bricked’ log).

***Total Phase Time*: Before** human visitation, 3 % of the total phase time of phases of known duration for all duration classes together (*indCats-allScls*; ‘bricked’ logs in fig. 5.3.3-3a) were assigned to the behaviour system of ‘comfort’. **During** visitation, the proportion dropped to 1 %. The re-increase **after** visitation (to 4 %) exceeded pre-visit proportions.

***Category Phase Number*:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-3a), the greatest proportion of phases of comfort behaviour was assigned to the subclass 03-10 s in **all periods** (54 %, 76 %, and 44 %, resp.).

Pre-visit, 85 % of all phases of comfort behaviour fell into the short-durations class, while the remaining 15 % were assigned to the class comprising medium durations (with the first and third subclass ‘occupied’) and the long-durations class was ‘unoccupied’ . **During-visit** proportion of numbers of phases of comfort behaviour assigned to the short-durations class increased by 10 % (to 95 %). Proportions for the medium-durations class decreased to 5 % (with only the first subclass ‘occupied’). **Post-visit**, there was a 12 % decrease in the short-durations class (to 83 %), accompanied by an increase in the medium-durations class (to 17 %, with phase durations assigned to each of the three subclasses).

In terms of **recovery** (comparing pre- to post-visit values), the short-durations class held 2 % less of all phases of comfort behaviour after visitation than prior to visitation, while the class of medium

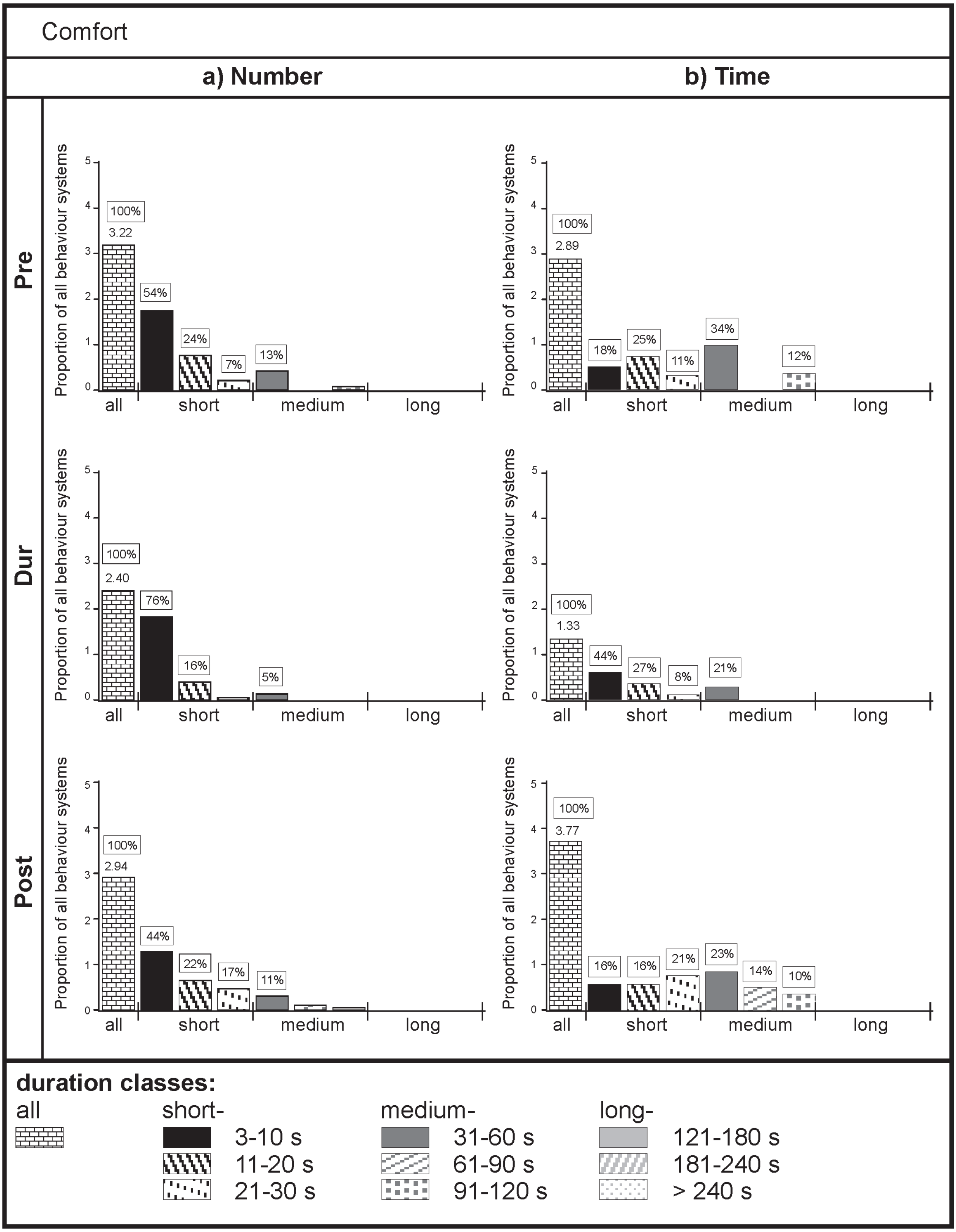

Figure 5.3.3-3 a) and b): Proportions of Duration Subclasses for the Behaviour Category <u>'comfort'</u>: a) Phase Number (left) and b) Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first ('bricked') log show proportion of 'comfort' with respect to <u>total</u> phase number and time (all phases from all categories = 100 %); %-values above logs represent proportions of <u>category</u> phase number and time (all phases of 'comfort' = 100 %). Number: total phase number, Time: total phase time; all = all duration (sub-)classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 46 phases, 746 s; during-visit: 37 phases, 314 s; post-visit: 54 phases, 1030 s.

durations was augmented by 2 %. Within both classes, a tendency towards longer phase durations was evident.

***Category Phase Time*:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-3b), phases assigned to the subclass 31-60 s (shortest of the medium-durations class) accounted for the greatest proportion of time **prior to** and **after** visitation (34 %, and 23 %, resp.). In contrast, the greatest proportion of time **during** visitation resulted from phases of the subclass 03-10 s (44 %).

Prior to visitation, phases of comfort behaviour in the short-durations class accounted for 54 % of the overall time spent in this behaviour system, 46 % of the time was taken up by phases assigned to the medium-durations class (fig. 5.3.3-3b), and the log-durations class was 'unoccupied'. **During-visit** proportions of time of phases in the short-durations class increased by 25 % (to 79 %), while proportions of time of phases assigned to the medium-durations class decreased to 21 %. **Post-visit**, there was a 26 % decrease in proportion of time of phases assigned to the short-durations class (to 53 %), complemented by an increase in proportions of time of phases sorted into the medium-durations class (to 47 %).

In terms of **recovery** (comparing pre- to post-visit values), differences in proportion of time assigned to phases of either class did not exceed 1 %. Within each class, however, a greater proportion of the time came from subclasses of longer durations after visitation than prior to visitation.

5.3.3.2.4 Breed

Summing up, the overall proportion of phases of breeding behaviour for all duration classes (*indCats-allScls*, 'bricked' logs in fig. 5.3.3-4a and b) exhibited a slight increase (as compared to pre-visit) **during** visitation with respect number of phases, while time taken up by these phases remained approximately unchanged. **After** visitation, proportions increased further: Total phase number as well as total phase time after visitation exceeded pre-visitation proportions.

Within the category 'breed', the following between-period changes in individual duration classes were found (*indCats-indScls*; fig. 5.3.3-4a and b): **During** visitation, phases of short duration increased slightly in number (+1 %) as well as time taken up (+5 %), while phases of medium duration decreased. **After** visitation, a within-class shift towards longer phases was evident in short- and medium-durations classes for phase numbers as well as phase time. In the medium-durations class, the second subclass (61-90 s) was 'occupied' after visitation only.

The **overall amount** of breeding behaviour was **augmented** after visitation; additionally, **phases** tended to be **longer** than prior to visitation.

Following, results are presented in detail.

***Total Phase Number*: Before** human visitation, 7 % of the total phase number of phases of known duration for all duration classes together were assigned to the behaviour system of 'breed' (*indCats-allScls*, 'bricked' logs in fig. 5.3.3-4a). **During** visitation, the proportion increased to 8 %. Unlike other behaviours, the increase continued **after** visitation, and breeding behaviour accounted for 10 % of all phases of known duration post-visit so that the term 'recovery' does not apply here[6].

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[6] ... nor does the term 'incomplete recovery' introduced in chapter 5.3.2, as it implied a return towards pre-visit levels (e.g., still lower than pre-, only less so). Strictly speaking, the term 'overshooting' is not quite correct either, since it indicated a change in direction (e.g., decrease from pre- to during-, re-increase beyond pre-visit from during- to post-visit).

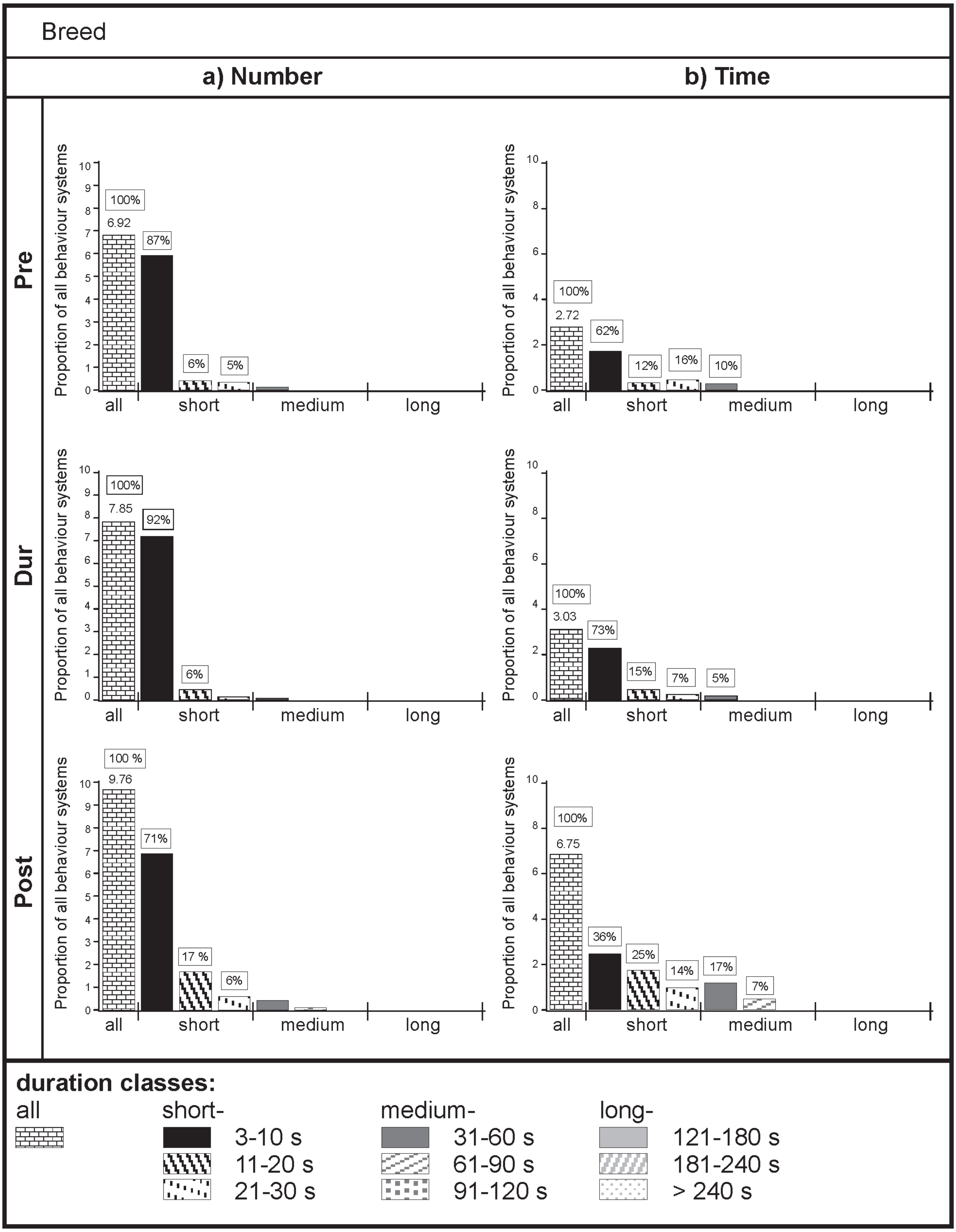

Figure 5.3.3-4 a) and b): Proportions of Duration Subclasses for the Behaviour Category '<u>breed</u>': a) Phase Number (left) and b) Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first ('bricked') log show proportion of 'breed' with respect to <u>total</u> phase number and time (all phases from all categories = 100 %); %-values above logs represent proportions of <u>category</u> phase number and time (all phases of 'breed' = 100 %). Number: total phase number, Time: total phase time; all = all duration (sub-)classes combined; short- / medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 99 phases, 702 s; during-visit: 121 phases, 714 s; post-visit: 179 phases, 1843 s.

Total Phase Time**: Before** human visitation, 3 % of the total phase time of phases of known duration for all duration classes together were assigned to the behaviour system of ‘breed’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-4b). **During** visitation, the proportion remained approximately unchanged. It increased **after** visitation (to 7 %), thus exceeding pre-visit proportions by 4 %.

Category Phase Number**:** With respect to distribution across individual duration subclasses (*indCats-indScls*), the greatest proportion of phases of known duration was assigned to the subclass 03-10 s in **all periods** (87 %, 92 %, and 71 %, resp.; fig. 5.3.3-4a).

Pre-visit, 98 % of all phases of breeding behaviour fell into the short-durations class, while the remaining 2 % were assigned to the class comprising medium durations (with only the first subclass ‘occupied’). The long-durations class was ‘unoccupied throughout’. **During-visit** proportion of number of phases of breeding behaviour assigned to the short-durations class increased by 1 % (to 99 %), while proportion for the medium-durations class decreased to 1 %. **Post-visit**, there was a 5 % decrease in the short-duration class (to 94 %), complemented by an increase in the medium-durations class (to 6 %, with ‘occupation’ of subclasses one and two).

Instead of **recovery** (comparing pre- to post-visit values), the continuous increase in numbers of breeding phases led to a 4 % reduction of phases assigned to the short-durations class, complemented by an increase of 4 % in the medium-durations class. Furthermore, within that class, the second subclass (61-90 s) had not been ‘occupied’ prior to visitation.

Category Phase Time**:** With respect to distribution across individual duration subclasses (*indCats-indScls*), the greatest proportion of time resulted from phases of the subclass 03-10 s (62 %, 73 %, and 36 %, resp.) in **all periods** (fig. 5.3.3-4b).

Pre-visit, phases of breeding behaviour in the short-durations class accounted for 90 % of the overall time spent in this behaviour system, and 10 % was taken up by phases assigned to the medium-durations class. **During-visit** proportion of time of phases in the short-durations class increased by 5 % (to 95 %), while proportion of time of phases assigned to the medium-durations class decreased to 5 %. **Post-visit**, there was a 19 % decrease in proportion of time of phases assigned to the short-durations class (to 76 %), complemented by an increase in proportions of time of phases sorted into the medium-durations class (to 24 %). With respect to the behaviour system of ‘breed’, there was no **recovery** (comparing pre- to post-visit values): Phases assigned to the short-durations class accounted for 14 % less of the time after visitation than prior to visitation, while the proportion of time of phases of medium duration increased by 14 %. Additionally, a greater proportion of the time within the latter class came from the second subclass (61-90 s) which had not been ‘occupied’ at all prior to visitation.

5.3.3.2.5 Vigilance

Summing up, the overall proportion of phases of vigilance behaviour for all duration classes (*indCats-IndScls*, ‘bricked’ logs in fig. 5.3.3-5a and b) remained approximately unchanged (as compared to pre-visit), **during** and **after visitation** with respect to ***total phase number***.

Total phase time (time taken up by these phases), however, more than doubled from before to **during** visitation. **After** visitation, proportions of phase time re-decreased but failed to make a complete **recovery** (remaining increase: + 6 %).

Within the category ‘vigilance’, between-period changes in individual duration classes were prominent (*indCats-indScls*; fig. 5.3.3-5a and b): **During** visitation, phases of short duration decreased, both in number as well as time taken up, while phases of medium and long duration increased. **After** visitation, pre-visit proportions were more or less regained.

The **overall proportion of time spent** vigilant was **augmented** (post- compared to pre-visit), but the distribution of **phase durations** across duration (sub)classes after visitation was **similar** to that found prior to visitation.

Following, results are presented in detail.

Total Phase Number**:** **Before** human visitation, 42 % of the total phase number for all duration classes together were assigned to the behaviour system of ‘vigilance’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-5a). **During** as well as **after** visitation, the proportion remained approximately stable[7] (at 43 %, and 41 %, resp.; fig. 5.3.3-5a).

Total Phase Time**:** **Before** human visitation, 29 % of the total phase time for all duration classes together were assigned to the behaviour system of ‘vigilance’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-5b). **During** visitation, the proportion increased to 66 %. The re-decrease **after** visitation (to 35 %) did not result in a complete **recovery**.

Category Phase Number**:** With respect to distribution across individual duration subclasses (*indCats-indScls*), the greatest proportion of phases of vigilance was assigned to the subclass 03-10 s (shortest of the short-durations class) in **all periods** (67 %, 43 %, and 65 %, resp.; fig. 5.3.3-5a).

Pre-visit, 92 % of all phases of vigilance fell into the short-durations class, 8 % were assigned to the class comprising medium durations, while the class of long durations held less than 1% (0.17 %). **During-visit** proportion of numbers of vigilance phases in the short-durations class decreased by 14 % (to 78 %), while proportions for the medium- and long-durations classes increased (to 19 %, and 2 %, resp.). **Post-visit**, there was a 14 % increase in the short-durations class (to 92 %), accompanied by decreases in medium- and long-durations classes (to 8 %, and <<1 %, resp.). In terms of **recovery** (comparing pre- to post-visit values), complete recovery was effected as regards proportion of number of phases in all three duration classes.

Category Phase Time**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-5b), phases assigned to the subclass 03-10 s accounted for the greatest proportion of time **prior to** and **after** visitation (30 %, and 29 %, resp.), whereas the greatest proportion of time **during** visitation resulted from phases of the subclasses 31-60 s (first subclass in the medium-durations class: 22 %).

Pre-visit, phases of vigilance in the short-durations class accounted for 64 % of the overall time spent vigilant, 33 % of that time was taken up by phases assigned to the medium-durations class, while only 2 % of overall time spent on vigilance resulted from phases of long durations. **During-visit** proportions of time of vigilance phases in the short-durations class decreased by 26 % (to 38 %). This was accompanied by an increase in proportions of time of vigilance phases assigned to the medium-durations (by 12 %, to 45 %) and, particularly, to the long-durations classes (by 15 %, to 17 %). **Post-visit**, there was a 27 % increase in proportions of time of phases assigned to the short-durations class (to 65 %), accompanied by decreases in proportions of time of phases sorted into medium- and long-durations classes (to 31 %, and 3 %, resp.).

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[7] rendering reflections on recovery rather pointless…

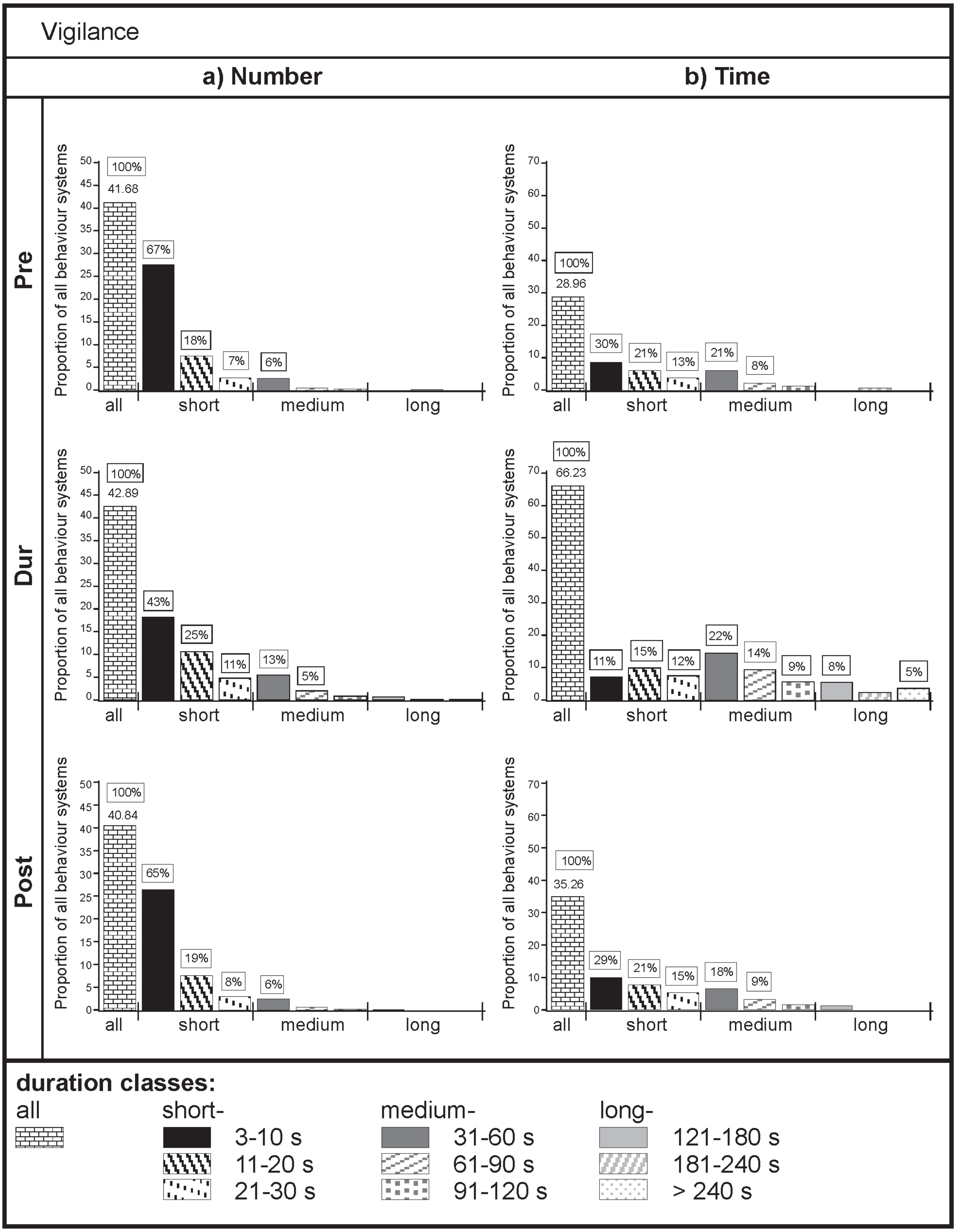

Figure 5.3.3-5 a) and b): Proportions of Duration Subclasses for the Behaviour Category <u>'vigilance'</u>: a) Phase Number (left) and b) Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first ('bricked') log show proportion of 'vigilance' with respect to total phase number and time (all phases from all categories = 100 %); %-values above logs represent proportions of category phase number and time (all phases of 'vigilance' = 100 %). Number: total phase number, Time: total phase time; all = all duration (sub-)classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 596 phases, 7482 s; during-visit: 661 phases, 15595 s; post-visit: 749 phases, 9629 s.

In terms of **recovery** (comparing pre- to post-visit values), proportion of time of phases assigned to short- and long-durations classes increased by 1 % each, while proportion of time of phases sorted into the medium-durations class decreased by 2 %. For the behaviour system of ‘vigilance’, recovery with respect to ***category phase time*** (distribution of phase durations across duration classes) was thus more or less complete – even though more overall time was devoted to vigilance.

5.3.3.2.6 Agonistics

Summing up, the overall proportion of phases of agonistic behaviour for all duration classes (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-6a and b) exhibited an increase (as compared to pre-visit) **during** visitation with respect to both number of phases recorded and time taken up by these phases. The increase in ***total phase number*** was more pronounced than the increase in ***total phase time***, indicating that increases had mainly consisted of additional short phases. **After** visitation, proportions re-decreased to approximately pre-visit level.

Within the category ‘agonistics’, the following between-period changes in individual duration classes were found (*indCats-indScls*; fig. 5.3.3-6a and b): **During** visitation, phases of very short duration (subclass 03-10 s) increased, both in number as well as time taken up, while phases of 11-20 s duration decreased. This indicated a change from defensive to offensive agonistic behaviour elements, as the latter take up considerably less time. Additionally, phases of 21-30 s, which had not been recorded prior to visitation, appeared during visitation. **After** visitation, a within-class shift towards longer phases was evident in the short-durations class; additionally, the first subclass of the medium-durations class (31-60 s) was ‘occupied’.

The **overall amount** of agonistic behaviour after visitation was **approximately equal** to that recorded prior to visitation, but **phases tended to be longer** in duration.

Following, results are presented in detail.

***Total Phase Number*:** **Before** human visitation, 5 % of the total phase number of phases of known duration for all duration classes together were assigned to the behaviour category of ‘agonistics’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-6a). **During** visitation, the proportion increased to 7 %. The re-decrease **after** visitation (to 5 %) led to a complete **recovery** with respect to total phase number.

***Total Phase Time*:** **Before** human visitation, 2 % of the total phase time of phases of known duration for all duration classes together were assigned to the behaviour category of ‘agonistics’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-6b). **During** visitation, the proportion increased to 3 %. It decreased to pre-visit proportions **after** visitation (2 %).

***Category Phase Number*:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-6a), the subclass 03-10 s (shortest of the short-durations class) held the greatest proportion of phases of known duration in **all periods**, and only a very small proportion was found in any other subclass. The long-durations class remained ‘unoccupied’ throughout.

Pre-visit and **during-visit**, 100 % of all phases of agonistic behaviours fell into the short-durations class. While **pre-visit** 92 % and 8 % fell into the first and second subclass, respectively, the first subclass contained 97 % of all phases **during** visitation indicating a change from defensive to offensive agonistic behaviour elements, as the latter take up considerably less time. Additionally, a small proportion of phases was assigned to the third subclass during visitation. **Post-visit**, 1 % of all phases shifted into the medium-durations class.

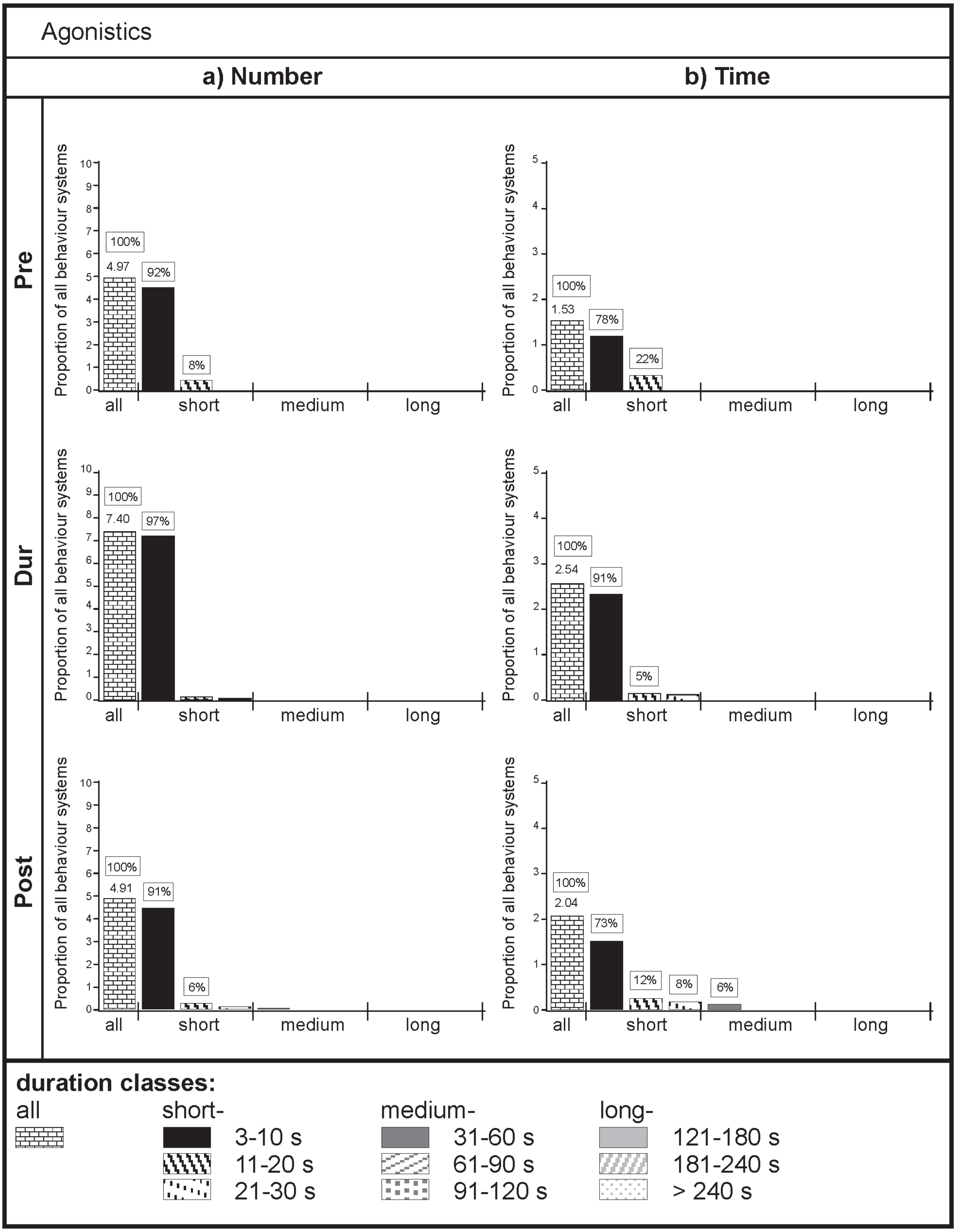

Figure 5.3.3-6 a) and b): Proportions of Duration Subclasses for the Behaviour Category 'agonistics': a) Phase Number (left) and b) Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first ('bricked') log show proportion of 'agonistics' with respect to total phase number and time (all phases from all categories = 100 %); %-values above logs represent proportions of category phase number and time (all phases of 'agonistics' = 100 %). Number: total phase number, Time: total phase time; all = all duration (sub-)classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 71 phases, 394 s; during-visit: 114 phases, 599 s; post-visit: 90 phases, 557 s.

In terms of **recovery** (comparing pre- to post-visit values), the shortest duration subclass was nearly unaffected (-1 %), while proportions assigned to the second shortest subclass (11-20 s: 8 % pre-visit; 6 % post-visit) were slightly reduced, and a small proportion (2 %) was found in the third subclass (21-30 s). Furthermore, the medium-durations class (1 % post-visit) had not been ‘occupied’ at all prior to visitation.

For the behaviour category of ‘agonistics’, there was thus a tendency towards **longer, but not more, phases** of agonistic behaviour after human visitation.

Category Phase Time**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-6b), the greatest proportion of time resulted from phases of the subclass 03-10 s in **all periods**.

Pre-visit and **during-visit**, phases of agonistic behaviour in the short-durations class accounted for 100 % of the overall time spent in this behaviour system. **Pre-visit**, only the first and second subclasses contributed to phase time. **During-visit**, 4 % of overall time spent on agonistic behaviours was accounted for by the third subclass (21-30 s). **Post-visit**, phases of agonistic behaviour assigned to the medium-durations class amounted to 6 % of the overall time. In terms of **recovery** (comparing pre- to post-visit values), proportion of time of phases assigned to the subclasses 03-10 s, and 11-20 s decreased by 5 %, and 10 %, resp. This was complemented by proportions of time of phases allotted to (sub-)classes not ‘occupied’ prior to human visitation, viz., to the subclass 21-30 s (8 %), and the first median-durations subclass (31-60 s: 6 %).

With respect to the behaviour category ‘agonistics’, **longer phases** after than prior to human visitation accounted for **more** of the **overall time** spent in this behaviour.

5.3.3.2.7 ‘Interruptions s.l.’

Recapitulation: Interruptions s.l. last a minimum of 3 s. They comprise behaviour elements from a minimum of two different behaviour systems, which change every one or two seconds. They are either flanked by the same behaviour system on both sides (‘within-phase interruptions’) or separate different behaviour systems (‘between-phase interruptions’). Interruptions end once behaviour from the same system has been shown for at least 3 s.

Summing up, the overall proportion of ‘interruptions s.l.’ for all duration classes (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-7a and b) exhibited a marked increase (as compared to pre-visit) **during** visitation with respect to both number of phases recorded and time taken up by these phases. **After** visitation, proportions re-decreased but remained slightly above pre-visit levels.

Within the category ‘interruptions s.l.’, the following between-period changes in individual duration classes were found (*indCats-indScls*; fig. 5.3.3-7a and b): **During** visitation, phases of very short duration (subclass 03-10 s) decreased, both in number as well as time taken up. Instead, more phases (both in numbers and time taken up) were found in the second subclass of the short-durations class (11-20 s), which had not been ‘occupied’ prior to visitation. **After** visitation, the vast majority of phases was still assigned to the subclass 03-10 s, but unlike pre-visitation, the second subclass (11-20 s) remained ‘occupied’.

The **overall amount** of ‘interruptions s.l.’ after visitation was **slightly higher** than that recorded prior to visitation, and **phases** tended to be **longer** in duration.

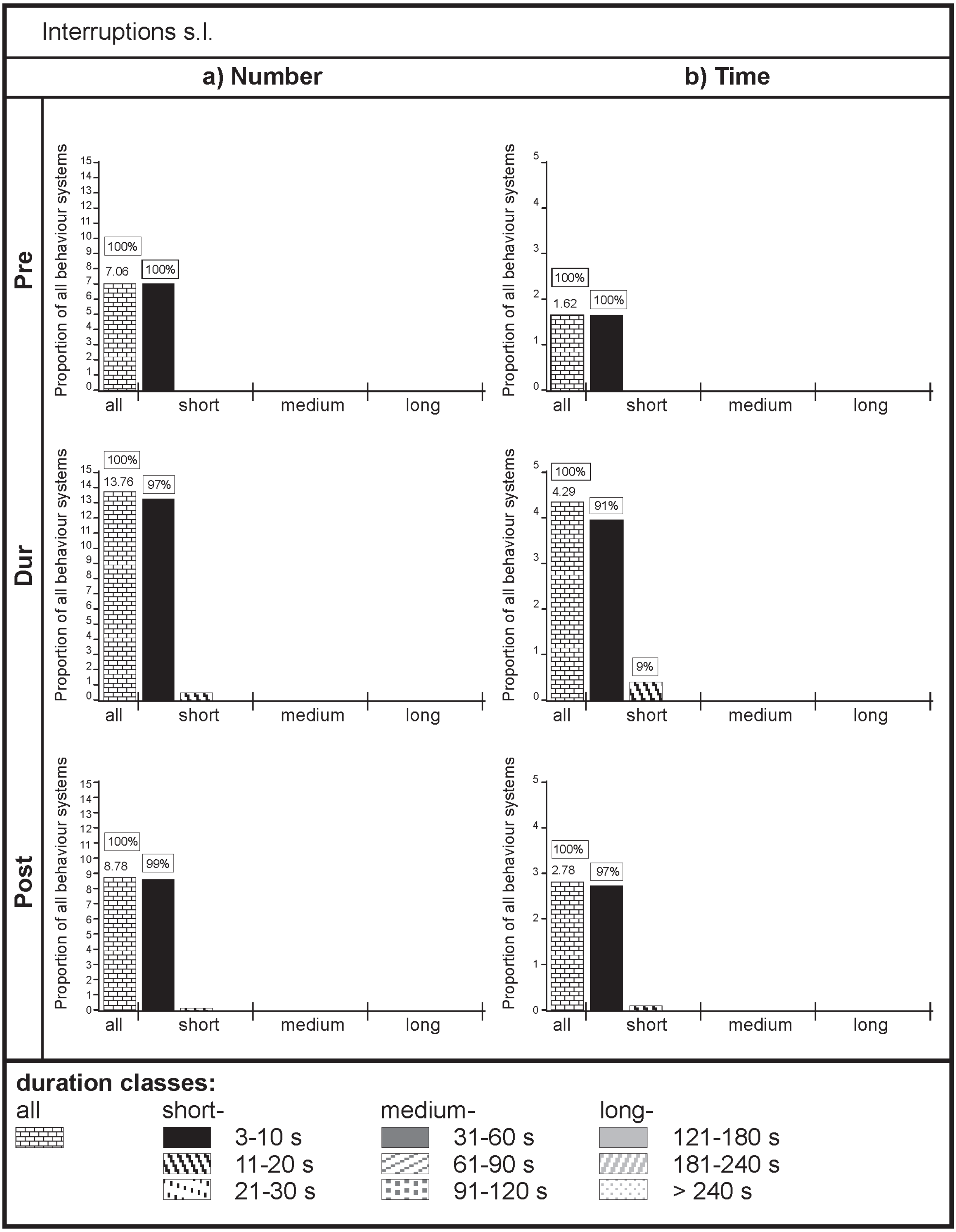

Figure 5.3.3-7 a) and b): Proportions of Duration Subclasses for the Behaviour Category <u>'interruptions s.l.'</u>: a) Phase Number (left) and b) Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first ('bricked') log show proportion of 'interruptions s.l.' with respect to <u>total</u> phase number and time (all phases from all categories = 100 %); %-values above logs represent proportions of <u>category</u> phase number and time (all phases of 'interruptions s.l.' = 100 %). Number: total phase number, Time: total phase time; all = all duration (sub-) classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 101 phases, 419 s; during-visit: 212 phases, 1009 s; post-visit: 161 phases, 759 s.

Following, results are presented in detail.

Total Phase Number**: Before** human visitation, 7 % of the total number of phases of known duration for all duration classes together were assigned to the behaviour category of ‘interruptions s.l.’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-7a). **During** visitation, the proportion increased to 14 %. The re-decrease **after** visitation (to 9 %) constituted an incomplete **recovery**.

Total Phase Time**: Before** human visitation, 2 % of the total time of phases of known duration for all duration classes together were assigned to the behaviour category of ‘interruptions s.l.’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-7b). **During** visitation, the proportion increased to 4 %. It decreased to 3 % **after** visitation, thus slightly exceeding pre-visit proportions.

Category Phase Number**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-7a), the subclass 03-10 s (shortest of the short-durations class) held the greatest proportion of phases of known duration in **all periods** (pre-: 100 %, during-: 97 %, post-: 99 %). Both medium- and long-durations class were ‘unoccupied’ throughout.

In **all periods**, 100 % of all phases of ‘interruptions s.l.’ fell into the short-durations class. While only the first subclass was ‘occupied’ **prior to** human visitation, 3 %, and 1 % of the phases were assigned to the second subclass **during-** and **post-**visitation, respectively. In terms of **recovery** (comparing pre- to post-visit values), the shortest duration subclass decreased by (-1 %), while the second shortest subclass (11-20 s: not ‘occupied’ pre-visit) gained 1 %.

There was thus a slight tendency towards **longer**, but **not more**, phases of ‘interruptions s.l.’ after human visitation.

Category Phase Time**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-7b), the greatest proportion of time resulted from phases of the subclass 03-10 s in **all periods**.

In **all periods**, phases of ‘interruptions s.l.’ in the short-durations class accounted for 100 % of the overall time spent in this behaviour category. Pre-visit, only the first subclass contributed to phase time. **During-visit**, 9 % of overall time spent on ‘interruptions s.l.’ was accounted for by the second subclass 21-30 s. **Post-visit**, this proportion decreased to 3 %. In terms of **recovery** (comparing pre- to post-visit values), proportion of time of phases assigned to the subclass 03-10 s decreased by 3 %. This was complemented by proportions of time of phases allotted to the following subclass (11-20 s) which had not been ‘occupied’ prior to human visitation.

With respect to the behaviour category ‘interruptions s.l.’, **longer phases** accounted for **more** of the **overall time** spent on this category after than prior to human visitation.

5.3.3.2.8 Proportion of Within-Phase and Before-Phase Impurities

Recapitulation: The extent of impurity was expressed as a proportion of the duration of each phase: The greater the number seconds with behaviour elements not pertaining to the behaviour system of a given phase, the greater the proportion of impurity.

***Within-Phase Impurities*: Prior to** human visitation, 19 % of all phases contained more than a negligible proportion of elements not pertaining to the behaviour system expressed (impurity level >0.01%). **During** visitation, this proportion increased to 27 %, and **after** visitation, it re-decreased to 23 %.

***Before-Phase Impurities*: Prior to** human visitation, 7 % of all phases were preceded by elements from other behaviour systems resulting in none-negligible impurity levels (>0.01%). **During** visitation, this proportion increased to 9 %, and **after** visitation, it re-decreased to 8 %.

Summing up, proportion of ***within-phase*** impurities increased (as compared to pre-visit) **during** human visitation (by 8 %), and decreased again **after** visitation (by 4 %). In contrast, ***before-phase*** impurities did not markedly change **between periods**.

5.3.3.2.9 Posture States and Posture Changes

As changes in posture constituted changes from one state into the other and back (only two categories), **number of 'prone' and 'up' posture states** was either equal or differed by 1. (In 7 sessions, equal numbers of posture states were counted, while in 44 sessions, 'prone' states invariably had 'the upper hand'.)

Over the course of all 51 sessions (of 19 FA, tab. 5.3.3-4), 436 posture **states** (240 'prone', 196 'up'; appendix 5.3.3-2) were recorded: Of these, 92 states **changed** pre-visit, 135 during-visit (of which 34 had commenced before visitation), 158 post-visit (of which 17 had commenced before visitation, 34 during-visitation), and 51 extended beyond the end of the session. In 7 of the sessions mentioned last, no posture change took place throughout the entire session ('prone' throughout).

A **total** of 385 posture **changes** were thus recorded (= 436 posture states -51 states noted at the end of each session).

The **first posture change** occurred before visitation in 19 sessions, in a further 19 sessions, it occurred during visitation, in 6 sessions it occurred after visitation, and in 7 sessions no posture change was recorded at all (s.a.)

If number of posture changes is weighted by period duration to permit comparison between change rates per period, results show that **rate of posture changes** was higher **during** (40 %) and **after** (37 %) than **prior to visitation** (24 %; appendix 5.3.3-2).

Changes were analysed by **Friedman-test** and revealed highly significant between-period differences (χ^2-value: 13.000, p=0.002, n=51). Follow-up pair-wise tests showed this to result from differences between pre- and during-visit frequencies (χ^2-value: 15.158, p=0.000, n=51).

During visitation, the **stages**[8] 'Visitor at 5 m' (44 % of all during-visit changes) and 'visitor at 3 m' (23 % of all during-visit changes) elicited a greater response than the stage 'Visitor at 15 m (16 %

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[8] Proportions of 'approach to' and 'time spent at' the respective distances have been added.

of all during-visit changes). This finding confirms the impression gained during visual appraisal (cf. chapter 5.3.1).

In all sessions recorded, **posture states extended across periods** (pre- to during-visitation, during- to post-visitation, pre- to post-visitation):

34 states extended from pre- to during-visitation (27 ’prone’, 7 ’up’),

34 states extended from during- to post-visitation (30 ’prone’, 4 ’up’), and

17 states extended from pre- to post-visitation (all ‘prone’).

Of the latter, 7 constituted sessions without any changes in posture state, in 2 sessions, posture changes were observed prior to visitation only, in 6 sessions post-visitation only, and in the remaining 2 sessions, posture changes occurred both before and after visitation.

The number of **posture states that did not extend across periods** thus amounted to 351 (= 436 -34 -34 -17), of which 166 ’prone’ and 185 ’up’ states were recorded. The following results on between-period changes in proportions of **state number** and **state time** are based on these figures, i.e., **overlaps** have been **excluded**.

5.3.3.2.10 Total State Number and Total State Time for Both Postures

Summing up, results for individual duration classes across both postures showed that the long-durations class disappeared entirely **during** visitation (*allCats-indScls*; fig. 5.3.3-8a and b), while the medium-durations class, rather than the short-durations class, increased (as compared to pre-visit) in both total state number and, particularly, time. **After** visitation, proportions in the long-durations class were greater, and proportions in the short-durations class smaller than prior to visitation. The fact that proportion of ***total state number*** for the **short-durations** class decreased by 4 % during visitation, while proportion of ***total state time*** increased by 10 %, indicates within-class shifts towards longer durations for this class.

Following, results are presented in detail.

If proportions of ***total state number***[9] before, during and after human visitation are examined for individual duration classes but for both postures together (*allCats-indScls*; fig. 5.3.3-8a), the following between-period changes become apparent:

In **all periods**, the first duration subclass (1-10 s) contained the greatest proportion of all states of (35 % pre-visit, 32 % during-visit, and 32 % post-visit).

Pre-visit, 77 % of all states of fell into the short-durations class (1-60 s), 12 % were assigned to the class of medium durations (61-240 s), while the class of long durations (241- >480 s) accounted for 11 % of the states examined.

During-visit as well as **post-visit**, proportions of states sorted into the short-durations class decreased slightly (to 73 %, and 70 %, resp.), while those for the medium-durations class increased (to 27 %) during visitation, and re-decreased to above pre-visit level after visitation (to 18 %). The long-durations class entirely disappeared during visitation and re-increased beyond pre-visit level (to 13 %) after visitation had ended.

Looking at ***total state time*** (*allCats-indScls*, proportions of time taken up by the respective subclasses/ classes; fig. 5.3.3-8b:), the greatest proportion **before** and **after** human visitation was

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[9] of states of within-period dimension

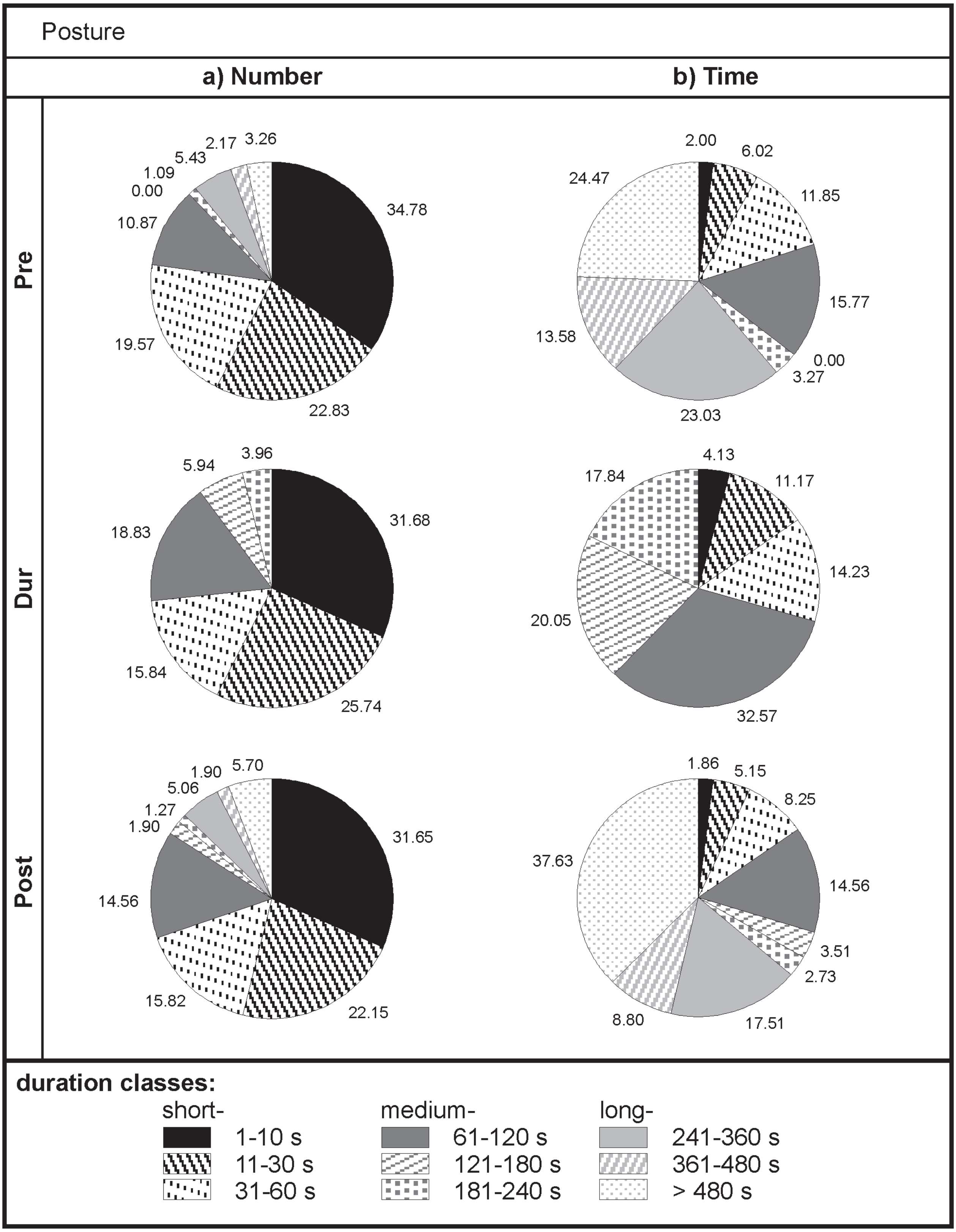

Figure 5.3.3-8 a) and b): Proportions of Duration Subclasses of a) Total State Number (left) and b) Total State Time (right) before (top), during (centre), and after (bottom) Human Visitation for both Posture Categories (‘prone’, ‘up’) Together. Number: total state number, Time: total state time; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 92 states, 6657 s; during-visit: 101 states, 4378 s; post-visit: 158 states, 13362 s.

assigned to the subclass of >480 s (third subclass of long durations: 24 %, and 38 %, resp.), while **during** visitation, the duration subclass of 61-120 s (first subclass of medium durations) accounted for the greatest proportion of time (33 %), and the long-durations class disappeared entirely.

Pre-visit, the short-durations class represented 20 % of ***total state time***; the medium-durations class held 19 %, and 61 % of ***total state time*** was assigned to the class of long durations.

During-visit, proportions of ***total state time*** accounted for by the short-durations class increased moderately (to 30 %), while those of medium-durations more than tripled (to 71 %). As mentioned above, the long-durations class disappeared entirely. **Post-visit**, proportions for the short-durations class decreased to below pre-visit level (to 15 %), proportions for the medium-durations class decreased to just above pre-visit level (to 21 %), while the long-durations class reappeared and accounted for a slightly greater proportion than had been found pre-visit (64 %).

5.3.3.2.11 Prone

Summing up, the overall proportion of states spent ‘prone’ for all duration classes (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-9a and b) decreased (as compared to pre-visit) **during** visitation with respect to both number of states recorded and time taken up by these states. **After** visitation, proportions re-increased and made a (nearly) complete **recovery**.

Within the category ‘prone’, between-period changes in individual duration classes were prominent (*indCats-indScls*; fig. 5.3.3-9a and b): **During** visitation, states of short and, particularly, medium duration increased, both in number as well as time taken up, while states of long duration disappeared. **After** visitation, states of long duration reappeared at a higher level than pre-visitation.

The **overall ‘amount’** of the posture ‘prone’ after visitation resembled that prior to visitation, with the exception of a **greater prominence** of states of the **longest durations** (>480 s).

Following, results are presented in detail.

***Total State Number*: Before** human visitation, 52 % of the total state number[10] for all duration classes together were assigned to the posture ‘prone’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-9a). **During** visitation, the proportion dropped to 39 %. The re-increase **after** visitation (to 50 %) approximated a complete **recovery**.

***Total State Time*: Before** human visitation, 83 % of the total state time for all duration classes together were assigned to the posture ‘prone’. **During** visitation, the proportion dropped to 41 %. The re-increase **after** visitation (to 83 %) resulted in a complete **recovery** (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-9b).

***Category State Number*:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-9a:), the greatest proportion of states of known duration was assigned to the subclass 1-10 s[11] in **all periods** (25 %, 36 %, and 21 %, resp.).

Pre-visit, 65 % of all states fell into the short-durations class, 15 % were assigned to the class comprising medium durations, while the class of long durations held 21%. **During-visit** proportion of number of states in the short- and medium-durations classes increased by 7 % (to 72 %) and 14 %[12] (to 28 %), respectively. The long-durations class disappeared entirely. **Post-visit**, there

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[10] of states of within-period dimension

[11] first subclass of the short-durations class

[12] pre: 14.58 %, increase by +13.62 % to 28.21 %

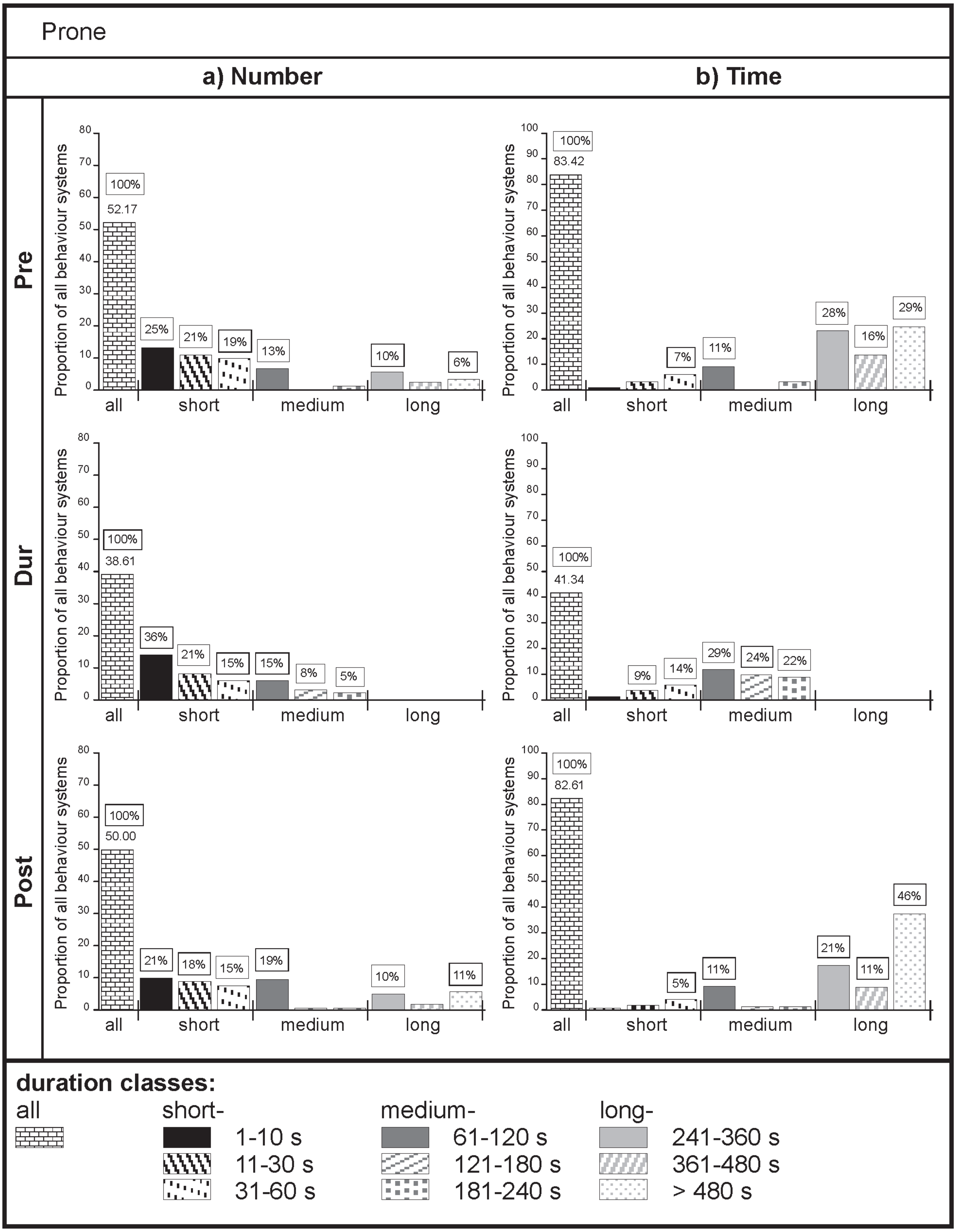

Figure 5.3.3-9 a) and b): Proportions of Duration Subclasses for the Posture Category ‘prone’: a) State Number (left) and b) State Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first (‘bricked’) log show proportion of ‘prone’ with respect to total state number and time (all states from both categories = 100 %); %-values above logs represent proportions of category state number and time (all states of ‘prone’ = 100 %). Number: total state number, Time: total state time; all = all duration (sub-)classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 48 states, 5553 s; during-visit: 39 states, 1810 s; post-visit: 79 states, 11039 s.

was a 19 % decrease in the short-durations class (to 53 %), and a 7 %[13] decrease in the medium-durations class (to 22 %). The long-durations class re-appeared at a higher level than that found prior to visitation (25 %).

In terms of **recovery** (comparing pre- to post-visit values), the short-durations class held 11 % less of all states after visitation than prior to visitation, while classes of medium and long durations were augmented by 7 % and 4 %, respectively.

Category State Time**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-9b), states assigned to the subclasses 241-360 s and >480 s[14] accounted for the greatest proportion of time **prior to visitation** (28 %, and 29 %, resp.), whereas these subclasses were entirely absent **during** visitation, and the greatest proportion of time was held by the subclass 61-120 s (29 %). **After** visitation, the greatest proportion (46 %) fell into the last durations subclass (>480 s).

Pre-visit, states in the short-durations class accounted for 12 % of the overall time spent <u>‘prone’</u>, 15 % of that time was taken up by states assigned to the medium-durations class, while 73 % of overall time spent <u>‘prone’</u> resulted from states of long durations. **During-visit** proportions of time of states in the short-durations class increased by 14 % (to 26 %) and the medium-durations class by 59 % (to 74 %), resulting in a complete disappearance of the long-durations class. **Post-visit**, there was an 18 % decrease in proportion of time of states assigned to the short-durations class (to 8 %), and a 59 % decrease in proportions of time of states sorted into the medium-durations class (to 15 %). The long-durations class reappeared, accounting for a higher proportion than pre-visit (77 %).

In terms of **recovery** (comparing pre- to post-visit values), proportion of time of states assigned to short-durations class decreased by 4 %, while proportion of time of states sorted into the long-durations class increased by the same amount. Within the long-durations class, the subclass of states exceeding 480 s was particularly prominent after visitation (increase from 29 % to 46 %), with complementary losses in the other subclasses. No change in proportion of time (pre-visit vs. post-visit) was found with respect to the class comprising medium durations.

<u>‘Prone’</u> states thus did **not** become **more**, **but** tended to last **longer**.

5.3.3.2.12 Up

<u>Summing up</u>, the overall proportion of states spent <u>‘up’</u> for all duration classes (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-10a and b) increased (as compared to pre-visit) **during** visitation with respect to both number of states recorded and particularly time taken up by these states. **After** visitation, proportions re-decreased, and a complete **recovery** was effected.

In the category <u>‘up’</u>, between-period changes in individual duration classes were prominent (*indCats-indScls*; fig. 5.3.3-10a and b): **During** visitation, states of short duration decreased, both in number as well as time taken up, while states of medium duration increased. **After** visitation, a shift back towards shorter durations occurred, but did not effect a complete **recovery**.

The **overall ‘amount’** of the posture <u>‘up’</u> resembled that prior to visitation, but **states** tended to be **longer** in duration.

Following, results are presented in detail.

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[13] dur: 28.21 %, decrease by -6.69 % to 21.52 %

[14] first and third subclass of the long-durations class

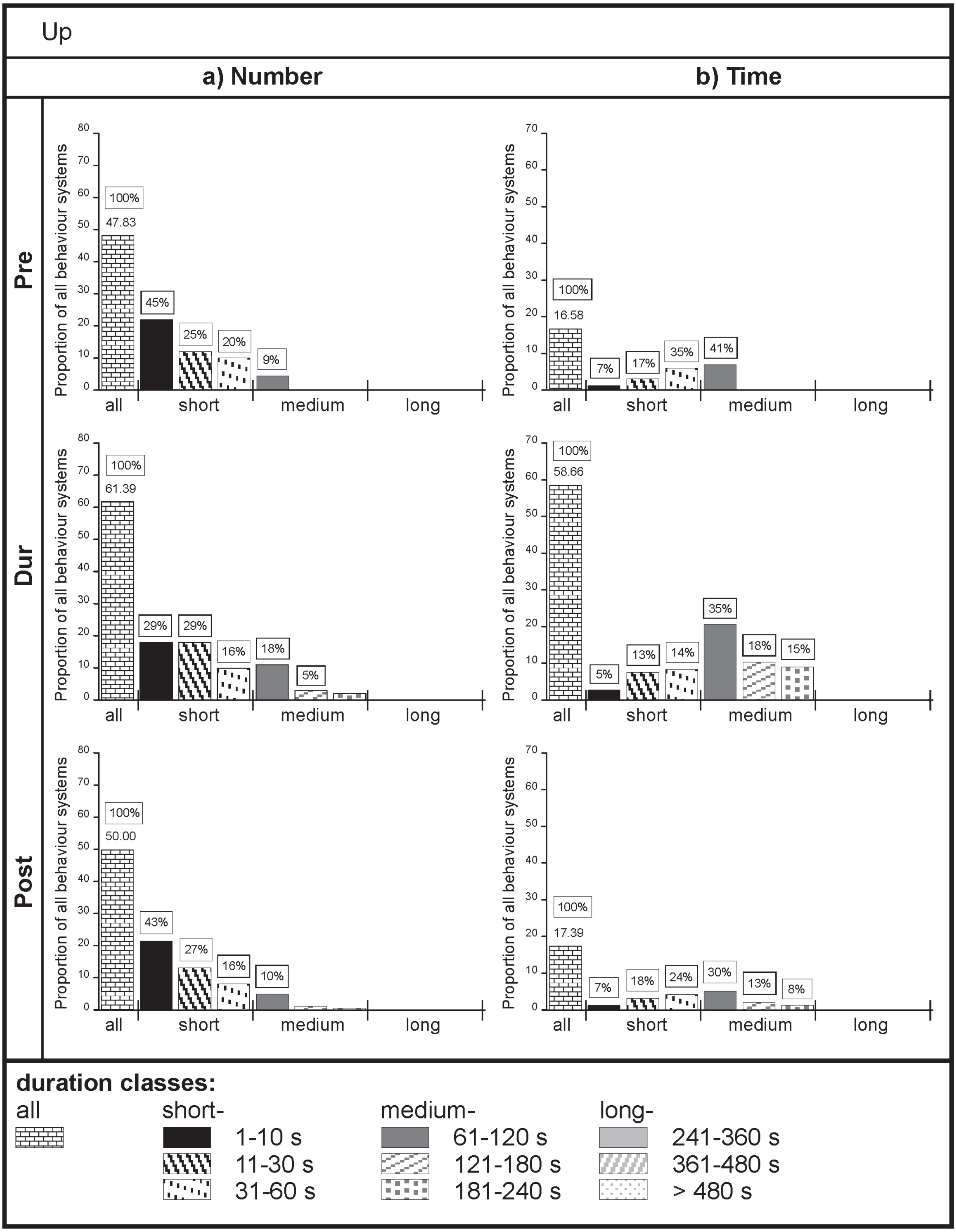

Figure 5.3.3-10 a) and b): Proportions of Duration Subclasses for the Posture Category 'up': a) State Number (left) and b) State Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first ('bricked') log show proportion of 'up' with respect to total state number and time (all states from both categories = 100 %); %-values above logs represent proportions of category state number and time (all states of 'up' = 100 %). Number: total state number, Time: total state time; all = all duration (sub-)classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 44 states, 1104 s; during-visit: 62 states, 2568 s; post-visit: 79 states, 2323 s.

Total State Number**: Before** human visitation, 48 % of the total state number[15] for all duration classes together were assigned to the posture <u>'up'</u> (*indCats-allScls*, 'bricked' logs in fig. 5.3.3-10a). **During** visitation, the proportion increased to 61 %. The re-decrease **after** visitation (to 50 %) approximated a complete **recovery**.

Total State Time**: Before** human visitation, 17 % of the total state time for *<u>all duration classes</u>* together were assigned to the posture <u>'up'</u> (*indCats-allScls*, 'bricked' logs in fig. 5.3.3-10b). **During** visitation, the proportion markedly increased (to 59 %). The re-decrease **after** visitation (to 17 %) resulted in a complete **recovery**.

Category State Number**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-10a), the greatest proportion of states of known duration was assigned to the subclass 1-10 s[16] **prior to** and **after** visitation (45 %, and 43 %, resp.), while **during** visitation the first and second (11-30 s) subclasses of the short-durations class held equal proportions (29 %). The class of long durations was 'unoccupied' in all periods.

Pre-visit, 91 % of all states fell into the short-durations class, and the remaining 9 % were assigned to the class comprising medium durations (to the first subclass only). **During-visit** proportion of number of states in the short-durations class decreased by 17 % (to 74 %), while proportions for the medium-durations class increased (to 26 %) with occupation of all three subclasses. **Post-visit**, there was a 12 % increase in the short-durations class (to 86 %), accompanied by a decrease in the medium-durations class (to 14 %). Of the latter, all three subclasses remained 'occupied', albeit at lower proportions than during visitation. In terms of **recovery** (comparing pre- to post-visit values), the short-durations class held 5 % less of all states after visitation than prior to visitation, while the class of medium was augmented by the same proportion. Additionally, the second and third subclasses of the medium-durations class were 'occupied' after, but not prior to visitation.

Category State Time**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-10b), states assigned to the subclass 61-120 s[17] accounted for the greatest proportion of time in **all periods** (41 %, 35 %, and 30 %, resp.). States of long durations were absent throughout.

Pre-visit, states in the short-durations class accounted for 59 % of the overall time spent <u>'up'</u>, and 41 % of that time was taken up by states assigned to the medium-durations class (to the first subclass only). **During-visit** proportions of time of states in the short-durations class decreased by 27 % (to 32 %). This was accompanied by an increase in proportions of time of states assigned to the medium-durations class (to 68 %) with all three subclasses 'occupied'. **Post-visit**, there was an 18 % increase in proportion of time of states assigned to the short-durations class (to 50 %), accompanied by a decrease in proportions of time of states sorted into the medium-durations class (to 50 %). In the latter, all three subclasses remained 'occupied'. In terms of **recovery** (comparing pre- to post-visit values), proportion of time of states assigned to short-durations classes decreased by 9 %, while proportion of time of states sorted into the medium-durations class increased by the same amount. Additionally, the second and third subclasses of the medium-durations class were 'occupied' after, but not prior to visitation.

<u>'Up'</u> states thus did **not** become **more**, **but** tended to last **longer**.

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[15] of states of within-period dimension

[16] first subclass of the short-durations class

[17] first subclass of the medium-durations class

5.3.3.2.13 Total Phase Number and Total Phase Time for All Heart Rate Categories

Summing up, results for individual duration classes across all heart rate categories (*allCats-indScls*) indicate a tendency towards reductions in phase duration from **before- to during-**visitation as well as from **during- to post-**visitation (with a greater number of shorter phases taking up more of overall time). In the short-durations class, ***total phase number*** increased by 2 % (during-visitation) plus 7 % (post-visitation), respectively. This was accompanied by a 4 % plus 9 % increase in ***total phase time*** assigned to this class (fig. 5.3.3-11a and b).

Time-wise, the complementary losses were located in the long-durations class only (with the medium-durations class increasing in proportions) both, **during** and **after** visitation. Complementary losses in ***total phase number*** **during** visitation occurred in the class comprising median durations, while **after** visitation, the greatest reduction was found in the long-durations class.

The fact that for the long-durations class proportion of ***total phase time*** decreased by 6 % **during** visitation while proportion of ***total phase number*** remained unchanged indicates within-class reductions in phase duration in addition to those extending across classes.

Following, results are presented in detail.

If proportions of ***total phase number*** before, during and after human visitation are examined for individual duration classes but for all categories together (*allCats-indScls*; i.e., irrespective of category), the following changes become apparent (fig. 5.3.3-11a and b):

In **all periods**, the first duration subclass (20 s) contained the greatest proportion of all phases of known duration (45 % pre-visit, 45 % during-visit, and 50 % post-visit).

Pre-visit, 70 % of all phases of known duration fell into the short-durations class (20-60 s), 20 % were assigned to the class of medium durations (80-240 s), while the class of long durations (260- >480 s) accounted for 10 % of the phases examined.

During-visit as well as **post-visit**, proportions of phases sorted into the short-durations class increased (to 72 %, and 78 %, resp.), while those for the medium-durations class decreased (to 18 %, and 16 %, resp.). The long-durations class remained unchanged **during** visitation and decreased to 5 % **after** visitation had ended.

Looking at ***total phase time*** (proportions of time taken up by the respective subclasses/ classes), the greatest proportion **before** and **during** human visitation were assigned to the subclass 260- >480 s s (third subclass of long durations: 37 %, and 21 %, resp.), while **after** visitation, approximately equal proportions were found in the first (20 s) and last (s.a.) duration subclasses (15 %, and 14 %, resp.).

Figure 5.3.3-11 also shows an ‘increasing equalisation’ of proportions for individual duration classes **during** (range: 4 % to 21 %) and, particularly, **after** (range: 7 % to 15 %) visitation (**pre-visit** range: 4 % to 37 %).

Pre-visit, the short-durations class represented 21 % of ***total phase time***; the medium-durations class held 25 %, and 54 % of ***total phase time*** were assigned to the class of long durations.

During-visit as well as **post-visit**, proportions of ***total phase time*** accounted for by the short-durations class increased (to 25 %, and 34 %, resp.). Those of the medium-durations class likewise increased, albeit at a lower level (to 26 %, and 32 %, resp.). In contrast, the long-durations class decreased (to 48 %, and 34 %, resp.), particularly after visitation.

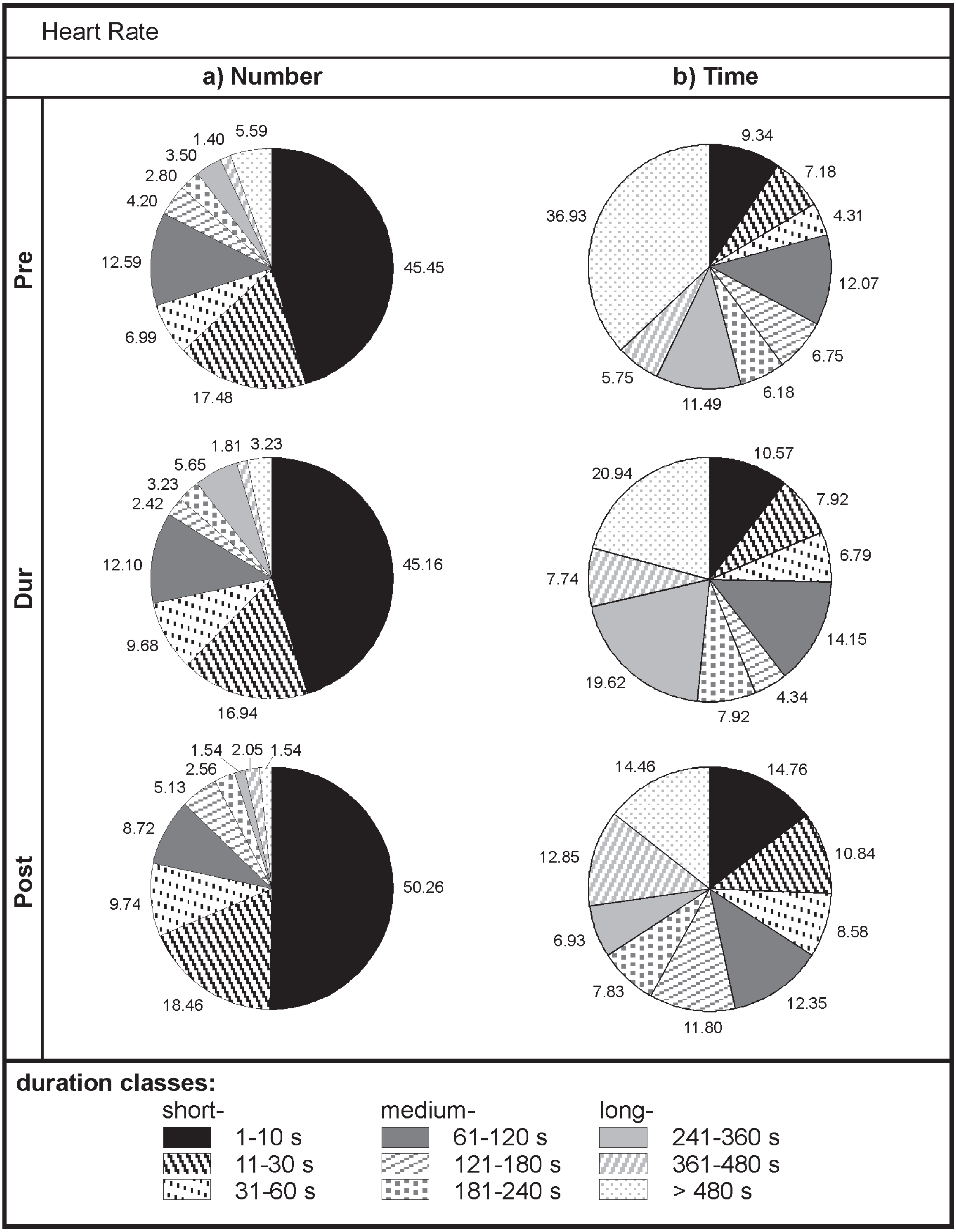

Figure 5.3.3-11 a) and b): Proportions of Duration Subclasses of a) Total Phase Number (left) and b) Total Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation for All Three Heart Rate Categories (‘below’, ‘within’, ‘above’) Together. Number: total phase number, Time: total phase time; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 143 phases, 13920 s; during-visit: 124 phases, 10600 s; post-visit: 195 phases, 13280 s.

5.3.3.2.14 Below Resting Heart Rate (±2 SD)

Summing up, the overall proportion of phases assigned to the heart rate category ‘below’ for all duration classes (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-12a and b:) **during** visitation remained approximately unchanged (decrease by <1 % as compared to pre-visit) with respect to number of phases recorded. Time taken up by these phases, however, nearly tripled. **After** visitation, proportion of numbers decreased very slightly, while proportion of time decreased but failed to make a complete **recovery**.

In the category ‘below’, between-period changes in individual duration classes were prominent (*indCats-indScls*; fig. 5.3.3-12a and b): **During** visitation, phases of short duration decreased, both in number and particularly time taken up, while phases of medium and long duration increased. **After** visitation, a general shift back towards shorter durations occurred (long-durations class ‘unoccupied’ once more), but did not effect a complete **recovery**: Phases of medium duration were more prominent (as compared to pre-visit), and within short- as well as medium-duration classes, higher subclasses received greater proportions than prior to visitation.

After visitation, the **overall amount** of the heart rate assigned to the category ‘below’ was very slightly **reduced** with respect to phase **numbers**, but **augmented** with respect to phase **time**: While proportion of **phases** was slightly reduced, phases tended to be **longer** in duration.

Following, results are presented in detail.

Total Phase Number**: Before** human visitation, 20 % of the total phase number[17] for all duration classes together were assigned to the heart rate category ‘below’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-12a:). **During** visitation, the proportion decreased very slightly to 19 %. **After** visitation a further decrease of similar magnitude (to 18 %) occurred so that **recovery** was not effected.

Total Phase Time**: Before** human visitation, 5 % of the total phase time for all duration classes together were assigned to the heart rate category ‘below’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-12b). **During** visitation, the proportion increased to 15 %. The re-decrease **after** visitation (to 9 %) did not result in a complete **recovery**.

Category Phase Number**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-12a), the greatest proportion of phases of known duration was assigned to the subclass 20 s[18] in **all periods** (79 %, 54 %, and 72 %, resp.).

Pre-visit, 96 % of all phases fell into the short-durations class, 4 % were assigned to the class comprising medium durations, while the class of long durations was completely ‘unoccupied’. **During-visit** proportion of number of phases in the short-durations class decreased by 13 % (to 83 %), while proportions for the medium-durations class increased (to 13 %, and the long-durations class held 4 % of all phases. **Post-visit**, there was an 11 % increase in the short-durations class (to 94 %), accompanied by decreases in medium- (to 6 %), and long-durations classes, with the latter vanishing entirely.

In terms of **recovery** (comparing pre- to post-visit values), the short-durations class held 2 % less of all phases after visitation than prior to visitation, while the class of medium durations was augmented by 2 %. No change between pre- and post-visit values (‘unoccupied’ both times) was found for the long-durations class. Within short- as well as medium-duration classes, however, a

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[17] of phases of known duration

[18] first subclass of the short-durations class

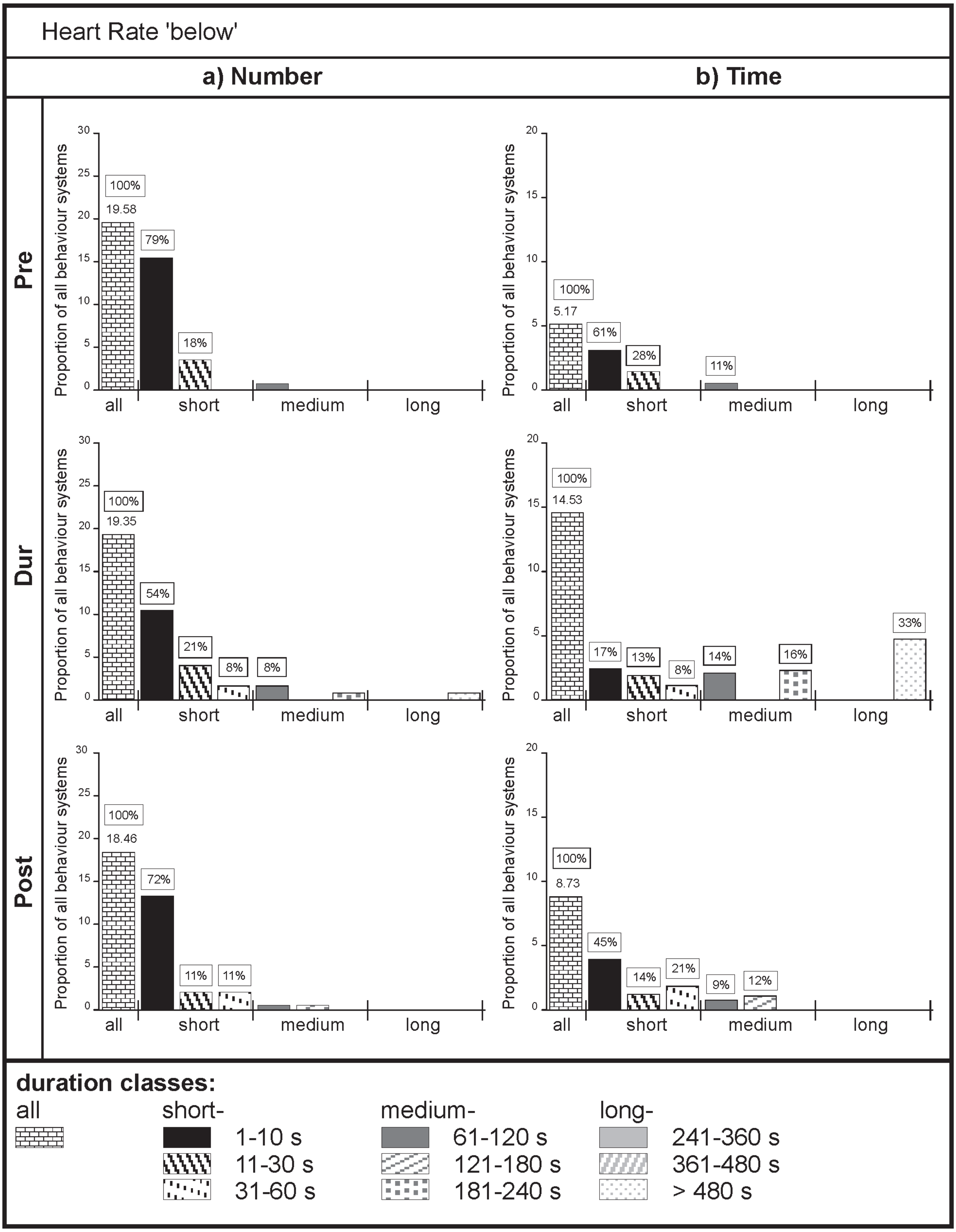

Figure 5.3.3-12 a) and b): Proportions of Duration Subclasses for the Heart Rate Category <u>'below'</u>: a) Phase Number (left) and b) Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first ('bricked') log show proportion of 'below' with respect to <u>total</u> phase number and time (all phases from all three categories = 100 %); %-values above logs represent proportions of <u>category</u> phase number and time (all phases of 'below' = 100 %). Number: total phase number, Time: total phase time; all = all duration (sub-)classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 28 phases, 720 s; during-visit: 24 phases, 1540 s; post-visit: 36 phases, 1160 s.

tendency towards longer phases became apparent (greater proportions in higher duration subclasses).

***Category Phase Time*:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-12b), phases assigned to the subclass 20 s[19] accounted for the greatest proportion of time **prior to** and **after** visitation (61 %, and 45 %, resp.), whereas the greatest proportion of time **during** visitation resulted from phases of the subclass >480 s (33 %).

Pre-visit, phases in the short-durations class accounted for 89 % of the overall time for the category ‘below’, 11 % of that time was taken up by phases assigned to the medium-durations class, while the long-durations class was ‘unoccupied’. **During-visit** proportions of time of phases in the short-durations class decreased markedly (by 51 %, to 38 %). This was accompanied by an increase in proportions of time of phases assigned to the medium-durations class (by 19 %, to 30 %) and, particularly, to the previously ‘unoccupied’ long-durations class (33 %). **Post-visit**, there was a 41 % increase in proportion of time of phases assigned to the short-durations class (to 79 %), accompanied by decreases in proportions of time of phases sorted into medium- and long-durations classes (to 21 %, and ‘complete disappearance’, resp.).

In terms of **recovery** (comparing pre- to post-visit values), proportion of time of phases assigned to short-durations classes decreased by 10 %, while proportion of time of phases sorted into the medium-durations class increased by the same amount. With respect to the class comprising long durations, no change in proportion of time was found (entirely ‘unoccupied’ pre- as well as post-visit).

5.3.3.2.15 Within Resting Heart Rate (±2 SD)

Summing up, the overall proportion of phases assigned to the heart rate category ‘within’ for all duration classes (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-13a and b) decreased (as compared to pre-visit) **during** visitation with respect to both number of phases recorded and particularly time taken up by these phases. **After** visitation, proportions re-increased. While **recovery** was approximately **complete** with respect to phase **numbers**, proportion of phase **time** remained considerably **reduced**.

In the category ‘within’, between-period changes in individual duration classes were prominent (*indCats-indScls*; fig. 5.3.3-13a and b): **During** visitation, phases of short duration increased, both in number as well as time taken up, while phases of long duration decreased. Phases of medium duration decreased in number but increased in time. **After** visitation, phases of short duration continued to increase in both number and time, albeit less ‘steeply’. Phases of medium duration decreased in both number and time, while phases assigned to the long-durations class remained unchanged in terms of number and slightly increased with respect to time. **Recovery** was thus far from effected. Phases exceeding 480 s were particularly affected by long-term reduction (from 43 % to 8 %).

While the **overall amount** of heart rate assigned to the category ‘within’ remained approximately **unchanged** with respect to phase **numbers**, the **time** spent in this category was **reduced** after visitation (as compared to pre-visit), as **phases** tended to be **shorter** in duration.

Following, results are presented in detail.

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[19] first subclass of the short-durations class

Total Phase Number**: Before** human visitation, 51 % of the total phase number of phases of known duration for all duration classes together were assigned to the heart rate category <u>‘within’</u> (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-13a). **During** visitation, the proportion dropped to 45 %. The re-increase **after** visitation (to 50 %) resulted in a (nearly) complete **recovery**.

Total Phase Time**: Before** human visitation, 85% of the total phase time for all duration classes together were assigned to the heart rate category <u>‘within’</u> (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-13b). **During** visitation, the proportion nearly halved (decrease to 43 %). The re-increase **after** visitation (to 61 %) did not result in a complete **recovery**.

Category Phase Number**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-13a), the greatest proportion of phases of known duration was assigned to the subclass 80-120 s[20] **prior to visitation** (23 %), but to the subclass 20 s[21] **during and after** visitation (45 %, and 35 %, resp.).

Pre-visit, 44 % of all phases fell into the short-durations class, 37 % were assigned to the class comprising medium durations, while the class of long durations contained 19 %. **During-visit** proportion of number of phases in the short-durations class increased by 20 % (to 64 %), while proportions for the medium- and long-durations classes decreased (to 29 %, and 7 %, resp.). **Post-visit**, there was a further 4 % increase in the short-durations class (to 68 %), accompanied by a decrease in the medium-durations class (to 24 %). The long-durations class remained unchanged (7 %).

In terms of **recovery** (comparing pre- to post-visit values), the short-durations class held 25 %[22] more of all phases after visitation than prior to visitation, while classes of medium and long durations were reduced by 13 % and 12 %, respectively.

Category Phase Time**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-13b), phases assigned to the subclass >480 s accounted for the greatest proportion of time **prior to** visitation (43 %), whereas the greatest proportion of time **during** visitation resulted from phases of the subclass 80-120 s (22 %). **After** visitation there was no clear ‘favouring’ of any subclass: Subclass 380-480 s (at 16 %) was closely matched by subclasses 80-120 s (15 %) and 140-180 s (14 %).

Pre-visit, phases in the short-durations class accounted for 10 % of the overall time for the category <u>‘within’</u>, 29 % of that time was taken up by phases assigned to the medium-durations class, while 61 % of overall time resulted from phases of long durations. **During-visit** proportion of time of phases in the short-durations class increased by 13 % (to 23 %), while that of phases in the medium-durations class increased by 17 % (to 45 %). This was accompanied by a decrease in proportions of time of phases assigned to the long-durations class (-29 %, to 32 %). **Post-visit**, there was a further 3 % increase in proportion of time of phases assigned to the short-durations class (to 27 %), accompanied by a decrease in proportions of time of phases sorted into the medium-durations class (-7 %, to 39 %), and a slight re-increase in the long-durations class (+3 %, to 35 %).

In terms of **recovery** (comparing pre- to post-visit values), proportion of time of phases assigned to the short-durations class increased by 16 %, while proportion of time of phases sorted into the

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[20] first subclass of the medium-durations class

[21] first subclass of the short-durations class

[22] pre: 43.84 %; post: 68.37 %; increase: +24.53 %

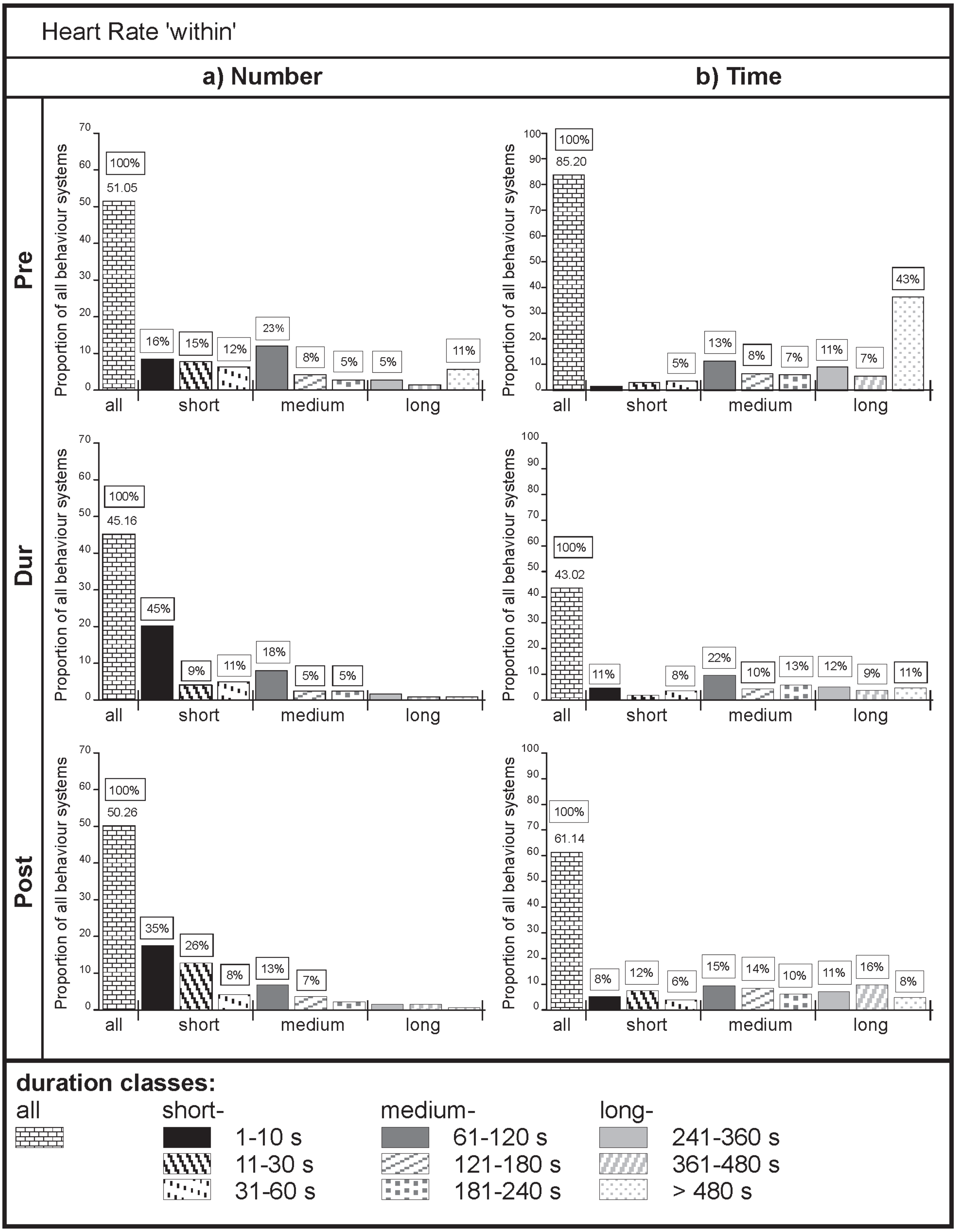

Figure 5.3.3-13 a) and b): Proportions of Duration Subclasses for the Heart Rate Category 'within': a) Phase Number (left) and b) Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first ('bricked') log show proportion of 'within' with respect to total phase number and time (all phases from all three categories = 100 %); %-values above logs represent proportions of category phase number and time (all phases of 'within' = 100 %). Number: total phase number, Time: total phase time; all = all duration (sub-)classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 73 phases, 11860 s; during-visit: 56 phases, 4560 s; post-visit: 98 phases, 8120 s.

medium-durations class increased by 10 %. As a consequence, proportion of time accounted for by the long-durations class decreased by 26 %. Within the long-durations class, the subclass of phases exceeding 480 s was particularly affected (decrease from 43 % to 8 %; fig. 5.3.3-13b).

Heart rate phases assigned to the category ‘within’ thus did **not** become **less**, **but** considerably **shorter**.

5.3.3.2.16 Above Resting Heart Rate (±2 SD)

Summing up, the overall proportion of phases assigned to the heart rate category ‘above’ for all duration classes (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-14a and b) increased (as compared to pre-visit) **during** visitation with respect to both number of phases recorded and particularly time taken up by these phases. **After** visitation, proportions re-decreased. While the proportion of phase numbers after visitation was approximately equal to that found prior to visitation, proportion of phase time post-visit was triple that found pre-visit. **Recovery** was thus far from complete.

In the category ‘above’, between-period changes in individual duration classes were prominent (*indCats-indScls*; fig. 5.3.3-14a and b): **During** visitation, phases of short duration decreased, both in number and particularly time taken up, while phases of medium and long duration appeared and increased, respectively. **After** visitation, a shift back towards shorter durations occurred, but did not effect a complete **recovery**.

After visitation, the **overall amount** of heart rate assigned to the category ‘above’ was **similar** to that found prior to visitation in terms of phase **numbers**, but **augmented** with respect to phase **time**: A more or less unchanged proportion of **phases** thus tended to be **longer** in duration.

Following, results are presented in detail.

Total Phase Number**: Before** human visitation, 29 % of the total phase number for all duration classes together were assigned to the heart rate category ‘above’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-14a). **During** visitation, the proportion increased to 35 %. The re-decrease **after** visitation (to 31 %) approximated a complete **recovery**.

Total Phase Time**: Before** human visitation, 10 % of the total phase time for all duration classes together were assigned to the heart rate category ‘above’ (*indCats-allScls*, ‘bricked’ logs in fig. 5.3.3-14b). **During** visitation, the proportion increased to 42 %. The re-decrease **after** visitation (to 30 %) constituted ‘anything but’ a complete **recovery**.

Category Phase Number**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-14a), the greatest proportion of phases of known duration was assigned to the subclass 20 s[23] in **all periods** (74 %, 41 %, and 62 %, resp.).

Pre-visit, 98 % of all phases fell into the short-durations class, while the class of long durations held 2%. The class comprising medium durations was ‘unoccupied’. **During-visit** proportion of number of phases in the short-durations class decreased by 23 % (to 75 %), while the proportion calculated for the long-durations class increased to 18 %, and the medium-durations class ‘acquired’ 7 %. **Post-visit**, there was a 10 % increase in the short-durations class (to 85 %). The medium-durations class increased to 10 %, while the long-durations class decreased to 5 %. In terms of **recovery** (comparing pre- to post-visit values), the short-durations class held 13 % less of all

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[23] first subclass of the short-durations class

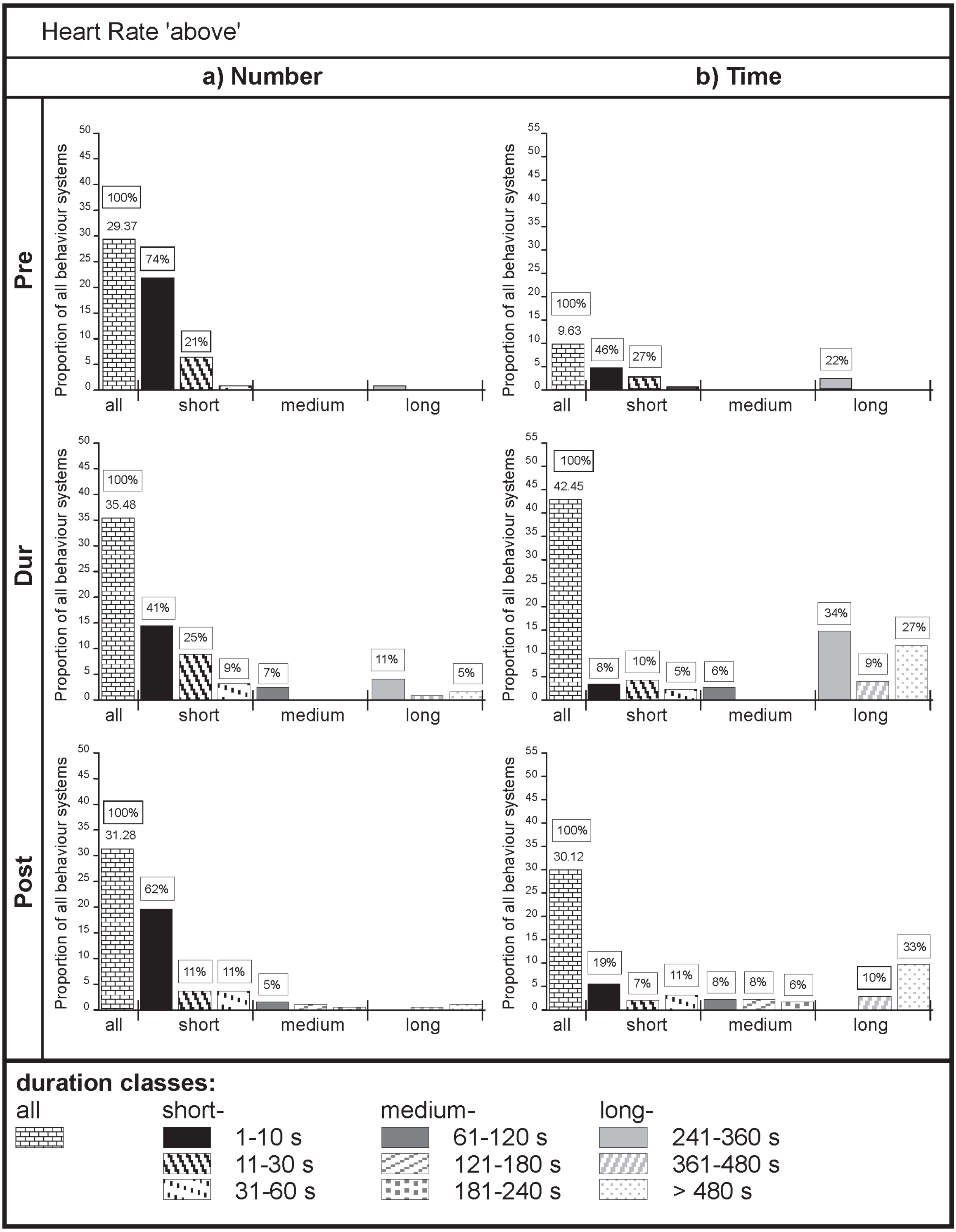

Figure 5.3.3-14 a) and b): Proportions of Duration Subclasses for the Heart Rate Category ‘above’: a) Phase Number (left) and b) Phase Time (right) before (top), during (centre), and after (bottom) Human Visitation. Scale on Y-axis and first (‘bricked’) log show proportion of ‘above’ with respect to total phase number and time (all phases from all three categories = 100 %); %-values above logs represent proportions of category phase number and time (all phases of ‘above’ = 100 %). Number: total phase number, Time: total phase time; all = all duration (sub-)classes combined; short-/ medium-/ long-: duration subclasses pertaining to the short-, medium-, and long-durations classes, resp.; Pre: before human visitation, Dur: during human visitation, Post: after human visitation; pre-visit: 42 phases, 1340 s; during-visit: 44 phases, 4500 s; post-visit: 61 phases, 4000 s.

phases after visitation than prior to visitation, while classes of medium and long durations were augmented by 10 % (previously unoccupied) and 3 %, respectively.

Category Phase Time**:** With respect to distribution across individual duration subclasses (*indCats-indScls*; fig. 5.3.3-14b), phases assigned to the subclass 20 s[24] accounted for the greatest proportion of time **prior to visitation** (46 %), whereas the greatest proportion of time **during** visitation resulted from phases of the subclass 260-360 s (34 %), followed by the subclass >480 s (27 %). **After** visitation, the latter held by far the greatest proportion of time (33 %).

Pre-visit, phases in the short-durations class accounted for 78 % of the overall time for the category ‘above’, 22 % of that time was taken up by phases assigned to the long-durations class, while the medium-durations class remained unoccupied. **During-visit** proportions of time of phases in the short-durations class decreased drastically (-55 %, to 23 %). This was accompanied by an increase (appearance) in proportions of time of phases assigned to the medium-durations class (6 %) and, particularly, to the long-durations class (by 48 %, to 71 %). **Post-visit**, there was a 13 % increase in proportion of time of phases assigned to the short-durations class (to 37 %), and a 15 % increase in proportion of time of phases sorted into the medium-durations class (to 21 %). Proportion of time of phases in the long-durations class was reduced by 28 % and accounted for 43 % of ***category phase time***.

In terms of **recovery** (comparing pre- to post-visit values), proportion of time of phases assigned to short-durations classes decreased by 41 %, while proportions of time of phases sorted into medium- and long-durations classes increased by 21 % and 20 %, respectively. Within each class, subclasses comprising longer phases were more prominent after than prior to visitation.

5.3.3.3 Between-Period Changes – Comparison of Visiting Regimes

Regime differences were examined for **selected parameters** only, and inclusion/ exclusion was based on phase numbers (TPN), rather than phase time (TPT): Not all behaviour categories had occurred with a frequency that permitted further splitting (according to visiting regime). Posture states were generally long and changed comparatively rarely (resulting in low numbers of states), so that splitting occurrences by regime, again, seemed preposterous[25]. They were consequently left out. With respect to heart rate, the category ‘below’ had occurred least often of the three categories (total phase number, TPN, FAs-allReg: 88[26]) and was likewise excluded.

For the same reason, differentiation according to phase duration (sub)classes was abandoned. For each of the categories chosen, results on regime differences are thus based on ***total phase number*** and ***total phase time***.

The behaviour categories chosen comprised resting (TPN: 1514) and vigilance behaviour (TPN: 2006) as well as ‘interruptions s.l.’ (TPN: 474). They were complemented by the heart rate categories ‘within[27]’ (TPN: 227) and ‘above’ (TPN: 147). Due to considerably lower numbers for heart rate categories, these results should be regarded as tentative at best.

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[24] first subclass of the short-durations class

[25] resp. preposturous

[26] all absolute figures available in appendix 5.3.3-1.02 to 5.3.3-1.04

[27] ‘within’ and ‘above’ resting heart rate ±2 SD

Tables 5.3.3-5 and 5.3.3-6 summarise the database used for behavioural and heart rate parameters, respectively. They show that chosen categories (larger font size) for behaviour as well as heart rate represent the majority of phases recorded for each period at each regime.

N.b.: With respect to heart rate phase durations obtained from group C, sessions were only available from dataset C_1.

Recapitulation: In terms of severity of **visiting regime**, loud and fast visitation (L&F) is hypothesised to exceed impact of silent and slow visitation (S&S), while 3 visitors (3 P) are assumed to exert a greater impact than 1 visitor (1 P). Ranking the regimes employed in this study, the following order would ensue:

3 P, L&F (FAs-Y) > 1 P, L&F (FAs-B_1; FAs-C_2) $\geq$ 3 P, S&S (FAs-X) > 1 P, S&S (FAs-C_1)

N.b.: In the text, FAs-$C_{1,2}$ will henceforth be summarily referred to as having been predominantly subjected to the regime 1 P, S&S, as next to no difference in behaviour had been observed in the first session following the switch in regimes (to 1 P, L&F), and heart rate records evaluated with respect to phases do not encompass the switch at all.

Summing up, this section examined graded responses to visiting regimes hypothesised to vary in severity of impact. Besides these graded responses, patterns that pointed to animal-mediated responses rather than regime-mediated ones were identified.

Regime differences were examined for **selected parameters** only, and inclusion/ exclusion was based on phase numbers, rather than phase time. Ranking order was based on magnitude of response relative to response levels obtained in a referential period (e.g., pre-visit for changes from pre- to during-visitation).

Between-period changes in ***total phase number*** were predominantly low in magnitude and did not single out any particular regime. The decrease in total phase number of the heart rate category 'above' found for FAs-Y from pre- to post-visitation was the only one to cross the 15 % threshold (at -15%) and thus to 'merit coloration' (according to colour code for proportional change classes).

Among the patterns observed, mirrored decreases (lowest referential proportion – lowest decrease, highest referential proportion – highest decrease) occurred with respect to the categories 'rest' and 'heart rate – within' (incompletely) from **pre- to during**-visitation, the category 'interruptions s.l.' from **during- to post-**visitation, and – albeit incompletely so – for the category 'vigilance' from **pre- to post**-visitation. In contrast, a measured decrease (highest referential proportion, lowest decrease) was found for the heart rate category 'above' from **during- to post-**visitation. Graded differences in impact of visiting regime were not discernable with respect to rankings of total phase number.

In terms of **recovery** (comparing pre- to post-visit proportions), those FAs that had been assigned the highest rank in pre-visit proportions of total phase number for each category invariably showed the most pronounced decrease in post-visit proportions. The opposite (lowest rank in pre-visit proportions resulting in an increase post-visit) was only observed with respect to the behaviour categories examined.

Concerning response propensities in terms of changes in total phase number, *overall propensity to respond* (pre- vs. during-visitation) seemed to be primarily animal-dependent, but might have been influenced by visitor conduct with respect to FAs-B_1 and FAs-Y (i.e., lower values for silent and slow regimes than for loud and fast ones), whereas *overall propensity to cease to respond* (during- vs. post-visitation) appeared to be animal-dependent rather than disturbance-mediated. In contrast, *overall propensity to continue to respond* beyond the withdrawal of disturbance stimulus (pre- vs. post-visitation) tallied with graded differences in impact of visiting regime.

Magnitudes of between-period changes in ***total phase time*** were considerably more pronounced than those observed for *total phase number*. The combination of comparatively small changes in phase number accompanied by greater changes in phase time was encountered with respect to the categories ‘rest’, ‘vigilance’ and ‘heart rate – within’, and was additionally found, albeit to a lesser extent, in the heart rate category ‘above’. Due to general brevity of phases in the category ‘interruptions s.l.’, this category was the only one for which total phase number altered in approximately the same magnitude as total phase time.

Among the patterns observed in changes of total phase time, mirrored decreases (lowest proportion – lowest decrease, highest proportion – highest decrease) occurred with respect to the categories ‘heart rate – within’ from **pre- to during**-visitation and ‘interruptions s.l.’ from **during- to post-**visitation. Incomplete measured increases were found for the heart rate category ‘above’ from **pre- to during-**visitation and for the category ‘rest’ from **during- to post-**visitation. Graded differences in impact of visiting regime were readily discernable with respect to rankings of total phase time for the categories ‘rest’, ‘vigilance’ and ‘heart rate – within’ from **pre- to during-**visitation. Graded differences were not apparent in changes observed from **during- to post-**visitation, but remained notable for the categories ‘rest’, and ‘vigilance’ (incompletely so) if **pre- and post-**visit proportions were compared. Additionally, differential responses to visitor conduct rather than visiting regime seemed likely with respect to the heart rate category ‘above’ from **pre- to during-**visitation and for both heart rate categories from **pre- to post-**visitation.

Concerning response propensities in terms of changes in total phase time, *overall propensity to respond* (pre- vs. during-visitation) reflected graded differences in impact of visiting regime, while *overall propensity to cease to respond* (during- vs. post-visitation) appeared to be animal-dependent rather than disturbance-mediated. In terms of **recovery**, *overall propensity to continue to respond* beyond the withdrawal of disturbance stimulus (pre- vs. post-visitation) seemed to be primarily linked to visitor conduct, with lower values for silent and slow regimes than for loud and fast ones. An additional impact of visitor number (1 vs. 3) was restricted to loud and fast regimes.

Following, results are presented in detail.

As regards ***total phase number*** per category, behaviour categories included comprise 75 % to 90 % of all phases per period (tab. 5.3.3-5), while heart rate categories contain between 62 % and 100 % (tab. 5.3.3-6).

With respect to ***total phase time*** per category, the respective proportions are between 80 % and 97 % for behaviour (tab. 5.3.3-5); they range from 58 % to 100 % for heart rate (tab. 5.3.3-6).

Rank orders suggested some response patterns not to be mediated by visiting regime or visitor conduct. These patterns and their potential interconnectedness with/ influence on graded responses are briefly illustrated below using ‘hypothetical FAs’ to depict the patterns.

Hypothesising four groups of FAs (E, G, O, R) visited in different manners, whereby regimes in decreasing order of impact are O (denoted as O^{imp-4}), G (G^{imp-3}), R (R^{imp-2}), and E (E^{imp-1}), the different patterns would lead to the rank orders depicted in table 5.3.3-7 (p. 378).

Table 5.3.3-5: Database for Comparison of Regimes – Selected Behaviour Categories. Counts of total phase number (TPN) and total phase time (TPT, in seconds) are presented for all behaviour categories pooled, followed by pooled proportions on the categories included (larger font size) and excluded (smaller font size) from comparisons. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_{1,2}$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-C$_2$: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F. pre: before human visitation, dur: during human visitation, post: after human visitation, tot: sum of all periods; %RVI: proportion of phases pertaining to the categories 'rest', 'vigilance' and 'interruptions s.l.'; %CBA: proportion of phases pertaining to the categories 'comfort', 'breed', and 'agonistics'. Proportions are based on total phase number/ time for all behaviour categories.

Visiting Regime	Period	Total Phase Number	Total Phase Time (s)	%RVI TPN	%RVI TPT	%CBA TPN	%CBA TPT
FAs-B$_1$	pre	406	7961	89.66	96.60	10.34	3.40
	dur	408	7849	86.52	95.73	13.48	4.27
	post	560	10081	85.54	91.14	14.46	8.86
	tot	**1374**	**25891**	**87.05**	**94.21**	**12.95**	**5.79**
FAs-C$_{1,2}$	pre	521	7133	85.99	91.66	14.01	8.34
	dur	489	6710	83.23	91.59	16.77	8.41
	post	594	7582	82.49	89.40	17.51	10.60
	tot	**1604**	**21425**	**83.85**	**90.84**	**16.15**	**9.16**
FAs-X	pre	359	7184	81.34	93.37	18.66	6.63
	dur	408	6053	81.13	92.93	18.87	7.07
	post	469	6953	80.81	83.00	19.19	17.00
	tot	**1236**	**20190**	**81.07**	**89.67**	**18.93**	**10.33**
FAs-Y	pre	144	3555	76.39	85.94	23.61	14.06
	dur	236	2933	75.42	89.77	24.58	10.23
	post	211	2695	77.25	79.55	22.75	20.45
	tot	**591**	**9183**	**76.31**	**85.29**	**23.69**	**14.71**
FAs-allReg	pre	1430	25833	84.90	92.87	15.10	7.13
	dur	1541	23545	82.35	93.09	17.65	6.91
	post	1834	27311	82.39	87.44	17.61	12.56
	tot	**4805**	**76689**	**83.12**	**91.00**	**16.88**	**9.00**

Mirrored decreases and measured increases constitute patterns in which FAs on the lowest rank for referential proportions exhibit the least pronounced decrease/ increase irrespective of treatment (regime), while FAs assigned the highest rank for referential proportions occupy the highest ranks for decreases (-4)/ increases (+4). While these patterns do represent a response to disturbance (in the sense of an effected change) they might be considered as primarily animal-dependent (degree of readiness to respond/ to cease responding) rather than disturbance-dependent (degree of impact to respond to/ to cease responding to).

To some extent, animal-dependent responses may be gauged by examining *overall propensity to respond*, expressed as the sum of absolute magnitudes (increases and decreases added).

In contrast, the pattern of measured decreases (whereby referential rank 1 is assigned to treatment rank -4, and referential rank 4 occupies treatment rank -1) might be thought of as disturbance-dependent rather than animal-dependent. If each 'conglomerate' of FAs responds similarly (in similar magnitude), however, this pattern does not necessarily display sensitivity towards regimes of different severity.

In the case of mirrored increases (whereby referential rank 1 is assigned to treatment rank +4 and referential rank 4 occupies treatment rank +1), responses might be regime-sensitive, but ceiling effects have to additionally be taken into account.

Table 5.3.3-6: Database for Comparison of Regimes – Selected Heart Rate Categories. Counts of total phase number (TPN) and total phase time (TPT, in seconds) are presented for all heart rate categories pooled, followed by pooled proportions on the categories included (larger font size) and excluded (smaller font size) from comparisons. FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-allReg: FAs from all regimes together (= sum FAs-B$_1$, FAs-C$_1$, FAs-X, FAs-Y). FAs-B$_1$: 1 P, L&F; FAs-C$_1$: 1 P, S&S; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F. pre: before human visitation, dur: during human visitation, post: after human visitation, tot: sum of all periods; %HR_w&a: proportion of phases pertaining to the categories 'within' and 'above' mean resting heart rate (RHR) ±2SD; %HR_b: proportion of phases pertaining to the category 'below' RHR ±2SD. Proportions are based on total phase number/ time for all heart rate categories.

Visiting Regime	Period	Total Phase Number	Total Phase Time (s)	%HR_w&a TPN	%HR_w&a TPT	%HR_b TPN	%HR_b TPT
FAs-B$_1$	pre	62	5020	80.65	94.42	19.35	5.58
	dur	55	5220	83.64	94.64	16.36	5.36
	post	80	6860	90.00	96.50	10.00	3.50
	tot	**197**	**17100**	**85.28**	**95.32**	**14.72**	**4.68**
FAs-C$_1$	pre	35	2360	74.29	90.68	25.71	9.32
	dur	34	1680	88.24	92.86	11.76	7.14
	post	50	2180	80.00	86.24	20.00	13.76
	tot	**119**	**6220**	**80.67**	**89.71**	**19.33**	**10.29**
FAs-X	pre	26	4180	73.08	94.74	26.92	5.26
	dur	21	2560	61.90	57.81	38.10	42.19
	post	28	2480	64.29	83.06	35.71	16.94
	tot	**75**	**9220**	**66.67**	**81.34**	**33.33**	**18.66**
FAs-Y	pre	20	2360	100.00	100.00	0.00	0.00
	dur	14	1140	78.57	94.74	21.43	5.26
	post	37	1760	78.38	88.64	21.62	11.36
	tot	**71**	**5260**	**84.51**	**95.06**	**15.49**	**4.94**
FAs-allReg	pre	143	13920	80.42	94.83	19.58	5.17
	dur	124	10600	80.65	85.47	19.35	14.53
	post	195	13280	81.54	91.27	18.46	8.73
	tot	**462**	**37800**	**80.95**	**90.95**	**19.05**	**9.05**

Table 5.3.3-7: Possible Response Patterns Obtained by Ranking FAs According to Order of Magnitude of Responses. 1 to 4: referential ranks (for proportions calculated pre-visit); -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease as compared to pre-visit; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase as compared to pre-visit., E, R, G, O: hypothesised groups of FAs subjected to visiting regimes of different impact, from imp-1 = least severe to imp-4 = most severe, measured: referential rank order prevails, mirrored: referential rank order is reversed.

	Pattern	**Rank Order – Decreases e.g., during-visit**				**Referential Rank Order e.g., pre-visit**				**Rank Order – Increases e.g., during-visit**			
		-4	**-3**	**-2**	**-1**	**1**	**2**	**3**	**4**	**+1**	**+2**	**+3**	**+4**
Decrease	Mirrored	R^{imp-2}	E^{imp-1}	O^{imp-4}	G^{imp-3}	G^{imp-3}	O^{imp-4}	E^{imp-1}	R^{imp-2}	n.a.			
	Measured	G^{imp-3}	O^{imp-4}	E^{imp-1}	R^{imp-2}	G^{imp-3}	O^{imp-4}	E^{imp-1}	R^{imp-2}	n.a.			
	Visiting Regime	O^{imp-4}	G^{imp-3}	R^{imp-2}	E^{imp-1}	G^{imp-3}	O^{imp-4}	E^{imp-1}	R^{imp-2}	n.a.			
Increase	Mirrored	n.a.				G^{imp-3}	O^{imp-4}	E^{imp-1}	R^{imp-2}	R^{imp-2}	E^{imp-1}	O^{imp-4}	G^{imp-3}
	Measured	n.a.				G^{imp-3}	O^{imp-4}	E^{imp-1}	R^{imp-2}	G^{imp-3}	O^{imp-4}	E^{imp-1}	R^{imp-2}
	Visiting Regime	n.a.				G^{imp-3}	O^{imp-4}	E^{imp-1}	R^{imp-2}	E^{imp-1}	R^{imp-2}	G^{imp-3}	O^{imp-4}

Last[28], but not least, a pattern of graded responses to treatment might result, if FAs respond predominantly regime-dependent, and most pronounced treatment rank is awarded to FAs subjected to the regime of highest severity (i.e., irrespective of reference rank order) followed by the other regimes in accordance with impact of visiting regime and/or visitor conduct.

5.3.3.3.1 Comparison of Between-Period Differences for Four Visiting Regimes with Respect to Total Phase Number and Time

To provide an overview on regime differences for all categories examined, results on total phase number and time have been summarised in tables 5.3.3-8a, 9a, 10a, and tables 5.3.3-8b, 9b, 10b, respectively. The colour codes for proportional classes and changes classes introduced in section **5.3.1.1** (tab. 5.3.1-6 and 5.3.1-7) facilitate recognition and comparison of magnitudes of referential proportions as well as changes.

Results on regime differences are based on total phase number and time for each of the five categories.

As already observed for between-period changes irrespective of regime (5.3.3.2), comparatively little alteration was observed with respect to ***total phase number***, and consequently, magnitudes of regime differences in total phase number are not particularly prominent either. In contrast, the change observed with respect to ***total phase time*** was of a substantially greater magnitude, than was that found for total phase number. Therefore, magnitudes of regime differences in total phase time were considerably more prominent as well.

As visualised in results across all regimes (5.3.3.2), small changes in phase number accompanied by greater changes in phase time invariably pointed to changes of phases in the medium- and/ or long-durations classes and thus led to substantial alterations in the structure of behaviour expressed.

Changes in *total phase number* from pre- to during-visitation: Magnitudes of change calculated for total phase number never exceeded ±14 % (no coloured change classes) at any of the regimes (tab. 5.3.3-8a).

Decreases in total phase number of the category ‘rest’ (tab. 5.3.3-8a: R) were observed in each regime. They constituted a mirrored decrease in that the least pronounced decrease was found for FAs-X with the lowest[29] pre-visit proportion, and the most pronounced decrease (FAs-B_1) corresponded to the highest pre-visit proportion. A similar pattern of ‘mirrored decreases’ occurred with respect to the heart rate category ‘within’ (tab. 5.3.3-8a: HR_w) – with the exception of FAs-$C_{1,2}$ (increase instead of decrease).

No such patterns in changes of total phase number were found for the categories ‘vigilance’ (tab. 5.3.3-8a: V), ‘interruptions s.l.’ (tab. 5.3.3-8a: I), and the heart rate category ‘above’ (tab. 5.3.3-8a: HR_a). As regards vigilance, slight or little pronounced increases in total phase number occurred in each regime. Concerning heart rate ‘above’, proportions increased for FAs-B_1 (pre-visit rank 3) and FAs-$C_{1,2}$ (pre-visit rank 2), remained approx. unchanged for FAs-X (pre-visit rank 1), and decreased for FAs-Y (pre-visit rank 4). As for ‘interruptions s.l.’, magnitude of increases was similar for FAs-$C_{1,2}$, FAs-B_1, and FAs-Y, and considerably lower for FAs-X. An influence of visitor conduct (loud and fast vs. silent and slow), however, cannot be discounted for FAs-Y (3 P, L&F) and, particularly, for FAs-B_1 (1 P, L&F).

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[28] Needless to say, the patterns outlined will generally boil down to a combination of animal- and disturbance-dependent responses.

[29] if proportions for FAs-X are not rounded off, they are lower than those found at FAs-Y

Overall propensity to respond in terms of changes in total phase number primarily reflected animal- rather than regime-differences: It was lowest for FAs-X (magnitudes of response summed up for increases and decreases together: 21), higher for FAs-$C_{1,2}$ (34), and highest for FAs-B_1 and FAs-Y (both 42). Again, visitor conduct, rather than the combination of visitor number and conduct, might account for higher response propensity with respect to FAs-B_1 and FAs-Y (both L&F).

Table 5.3.3-8a): Changes from Pre- to During-Visitation – Ranked Regime Differences in Total Phase Number (TPN) for Selected Behaviour and Heart Rate Categories. Values in **bold red** indicate rank order in concordance with hypothesised differences in severity of regime; values in red suggest conduct-mediated response differences. R: rest, V: vigilance, I: interruptions s.l., HR_w: heart rate within mean resting heart rate (RHR) ±2 SD, HR_a: heart rate above RHR ±2 SD; pre-visit: before human visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; 1 to 4: ranks for proportions calculated pre-visit; -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease as compared to pre-visit; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase as compared to pre-visit; change -1 % to +1 %: values with magnitudes of change lower than ±1 % were excluded from rankings and listed below the table. **N.b.:** If identical proportions appear in rank order, these differed in decimal values. Colour codes follow tab. 5.3.1-6 and tab. 5.3.1-7.

TPN		Decrease Ranks				%pre-visit				Increase Ranks			
		-4	-3	-2	-1	1	2	3	4	+1	+2	+3	+4
R	FAs	B_1	$C_{1,2}$	Y	X	X	Y	$C_{1,2}$	B_1				
	%	-13	-11	-11	-5	31	31	36	42				
V	FAs					Y	X	$C_{1,2}$	B_1		Y	B_1	X
	%					37	40	42	44		+1	+2	+3
I	FAs					B_1	$C_{1,2}$	Y	X	X	$C_{1,2}$	B_1	Y
	%					3	8	8	10	+2	+8	+8	+9
HR_w	FAs	**Y**	**X**	**B_1**		C_1	B_1	X	Y				C_1
	%	-12	-11	-8		46	52	54	55				+4
HR_a	FAs	Y				X	C_1	B_1	Y			C_1	B_1
	%	-9				19	29	29	45			+10	+11

Change -1 % to +1%: Vigilance, FAs-$C_{1,2}$ = +0.51 %; HR_a, FAs-X = -0.18 %

Changes in *total phase time* from pre- to during-visitation: Magnitudes of change calculated for total phase time were substantially higher (as compared to total phase number; tab. 5.3.3-8b), except for the parameter 'interruptions s.l.' (for which changes in total phase number exceeded those for total phase time).

Decreases in total phase time of the category 'rest' (tab. 5.3.3-8b: R) were observed in each regime. Unlike total phase number, these decreases tallied with hypothesised graded differences in impact of visiting regime (see recapitulation), in that the least pronounced decrease was found for FAs-$C_{1,2}$ (1 P, S&S), and the most pronounced decrease (FAs-Y) corresponded to the visiting regime 3 P, L&F, with FAs-X (3 P, S&S) occupying rank -2, and FAs-B_1 (1 P, L&F) being assigned to rank -3. Ranks for increased total phase time for the category 'vigilance' (tab. 5.3.3-8b: V), as well as decreased total phase time for the heart rate category 'within' (tab. 5.3.3-8b: HR_w) likewise suggested differences in impact of visiting regime, with FAs-$C_{1,2}$ exhibiting the least pronounced responses, while FAs-Y received the highest ranks. As regards vigilance, approximately similar response magnitudes for FAs-B_1 and FAs-X were found, whereas the category heart rate 'within' decreased more strongly for FAs-X than for FAs-B_1. Additionally, ceiling effects need to be taken into account with respect to vigilance, as rank order displayed the pattern of mirrored increase. Concerning the heart rate category 'above' (tab. 5.3.3-8b: HR_a), FAs exhibited a measured increase with the exception of FAs-Y (rank 2 to rank +4). In addition, impact of visitor conduct appears likely, as 'loud and fast' visitation (at FAs-B_1 and FAs-Y) ranked higher than 'silent and slow' visitation. Neither regime-dependent nor animal-dependent patterns in changes of total phase time were found for the category ‘interruptions s.l.’ (tab. 5.3.3-8b: I): Magnitude of increases was similar for FAs-$C_{1,2}$, FAs-B_1, and FAs-X, and higher for FAs-Y.

Overall propensity to respond in terms of changes in total phase time reflected hypothesised regime differences: It was lowest for FAs-$C_{1,2}$ (sum of absolute magnitudes of response: 73), higher for FAs-X (157) and FAs-B_1 (169), and highest for FAs-Y (233).

Table 5.3.3-8b): Changes from Pre- to During-Visitation – Ranked Regime Differences in Total Phase Time (TPT) for Selected Behaviour and Heart Rate Categories. Values in **bold red** indicate rank order in concordance with hypothesised differences in severity of regime; values in red suggest conduct-mediated response differences. R: rest, V: vigilance, I: interruptions s.l., HR_w: heart rate within mean resting heart rate (RHR) ± 2 SD, HR_a: heart rate above RHR ± 2 SD; pre-visit: before human visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; 1 to 4: ranks for proportions calculated pre-visit; -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease as compared to pre-visit; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase as compared to pre-visit; change -1 % to +1 %: values with magnitudes of change lower than ±1 % were excluded from rankings and listed below the table. **N.b.:** If identical proportions appear in rank order, these differed in decimal values. Colour codes follow tab. 5.3.1-6 and tab. 5.3.1-7.

TPT		Decrease Ranks				%pre-visit				Increase Ranks			
		-4	-3	-2	-1	1	2	3	4	+1	+2	+3	+4
R	FAs	**Y**	**B_1**	**X**	**$C_{1,2}$**	$C_{1,2}$	Y	B_1	X				
	%	-56	-45	-45	-21	44	68	69	70				
V	FAs					Y	X	B_1	$C_{1,2}$	**$C_{1,2}$**	**B_1**	**X**	**Y**
	%					17	22	27	45	+17	+42	+43	+55
I	FAs					B_1	Y	X	$C_{1,2}$	X	B_1	$C_{1,2}$	Y
	%					1	1	2	2	+2	+2	+3	+5
HR_w	FAs	**Y**	**X**	**B_1**	**C_1**	C_1	B_1	Y	X				
	%	-61	-52	-40	-15	78	81	91	91				
HR_a	FAs					X	Y	C_1	B_1	X	C_1	B_1	Y
	%					3	9	13	14	+15	+17	+40	+56

Change -1 % to +1%: not applicable

Changes in *total phase number* from during- to post-visitation: Magnitudes of change calculated for total phase number never exceeded ±14 % (no coloured change classes) at any of the regimes (tab. 5.3.3-9a).

Decreases in total phase number of the category ‘interruptions s.l.’ (tab. 5.3.3-9a: I) were observed in each regime. They constituted a mirrored decrease, in that the least pronounced decrease of total phase number was found for FAs-B_1 with the lowest during-visit proportion, and the most pronounced decrease was calculated for FAs-Y (highest during-visit proportion). Mirrored decrease led to very similar proportions[30] of post-visit total phase number for ‘interruptions s.l.’ among the regimes.

In contrast, a measured decrease (opposite pattern) was found for the heart rate category ‘above’ (tab. 5.3.3-9a: HR_a), in that higher during-visit proportions decreased less than lower proportions.

No such patterns were found for the categories ‘rest’ (tab. 5.3.3-9a: R), ‘vigilance’ (tab. 5.3.3-9a: V) and ‘heart rate – w’ (tab. 5.3.3-9a: HR_w). Total phase number of resting phases increased approximately equally in each regime, proportions of vigilance dropped slightly for FAs-B_1, FAs-X, and FAs-$C_{1,2}$, while they increased further for FAs-Y. With respect to the heart rate category ‘within’,

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[30] arrived at by subtracting decrease-values from during-visit values

proportions decreased for FAs-$C_{1,2}$ (thereby bouncing back to pre-visit level, e.g., tab. 5.3.3-8a), increased moderately for FAs-Y and FAs-B_1, and more strongly for FAs-X.

Overall propensity to cease responding in terms of changes in total phase number reflected animal- rather than regime-differences: It was highest for FAs-X (sum of absolute magnitudes of response: 41), lower for FAs-Y (32), and lowest for FAs-$C_{1,2}$ (23) and FAs-B_1 (22).

Table 5.3.3-9a): Changes from During- to Post-Visitation – Ranked Regime Differences in Total Phase Number (TPN) for Selected Behaviour and Heart Rate Categories. Values in **bold red** indicate rank order in concordance with hypothesised differences in severity of regime; values in red suggest conduct-mediated response differences. R: rest, V: vigilance, I: interruptions s.l., HR_w: heart rate within mean resting heart rate (RHR) ± 2 SD, HR_a: heart rate above RHR ± 2 SD; dur-visit: during human visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; 1 to 4: ranks for proportions calculated during-visit; -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease as compared to during-visit; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase as compared to during-visit; change -1 % to +1 %: values with magnitudes of change lower than ±1 % were excluded from rankings and listed below the table. **N.b.:** If identical proportions appear in rank order, these differed in decimal values. Colour codes follow tab. 5.3.1-6 and tab. 5.3.1-7.

TPN		Decrease Ranks				%dur-visit				Increase Ranks			
		-4	-3	-2	-1	1	2	3	4	+1	+2	+3	+4
R	FAs					Y	$C_{1,2}$	X	B_1	Y	B_1	$C_{1,2}$	X
	%					20	25	26	29	+6	+6	+7	+7
V	FAs	B_1	X	$C_{1,2}$		Y	X	$C_{1,2}$	B_1				Y
	%	-4	-4	-3		38	43	43	46				+5
I	FAs	Y	$C_{1,2}$	X	B_1	B_1	X	$C_{1,2}$	Y				
	%	-9	-5	-4	-3	11	13	15	17				
HR_w	FAs	C_1				n.a.	X; Y	B_1	C_1		Y	B_1	X
	%	-4				n.a.	43	44	50		+6	+8	+14
HR_a	FAs	X	Y	C_1	B_1	X	Y	C_1	B_1				
	%	-12	-6	-4	-1	19	36	38	40				

Change -1 % to +1%: not applicable

Changes in *total phase time* from during- to post-visitation: Magnitudes of change calculated for total phase time were substantially higher (as compared to total phase number; tab. 5.3.3-9b).

Increases in total phase time of the category ‘rest’ (tab. 5.3.3-9b: R) were observed in each regime. Unlike total phase number, these constituted a measured increase for all FAs except FAs-B_1, in that the lowest during-visit proportion received the lowest rank for increased post-visit resting. FAs-B_1 were exceptional in attaining highest ranks for total phase time with respect to increased rest as well as decreased vigilance. As already found for total phase number, a mirrored decrease in proportions of total phase time was observed for the category ‘interruptions s.l.’ (tab. 5.3.3-9b: I), again resulting in very similar post-visit proportions among the regimes with respect to this category. No patterns were found concerning the category ‘vigilance’ (tab. 5.3.3-9b: V), and the heart rate categories ‘within’ (tab. 5.3.3-9b: HR_w) and ‘above’ (tab. 5.3.3-9b: HR_a).

Overall propensity to cease responding in terms of changes in total phase time reflected animal- rather than regime-differences: It was highest for FAs-X (sum of absolute magnitudes of response: 119), lower for FAs-Y (110) and FAs-B_1 (107) and lowest FAs-$C_{1,2}$ (39).

Table 5.3.3-9b): Changes from During- to Post-Visitation – Ranked Regime Differences in Total Phase Time (TPT) for Selected Behaviour and Heart Rate Categories. Values in **bold red** indicate rank order in concordance with hypothesised differences in severity of regime; values in red suggest conduct-mediated response differences. R: rest, V: vigilance, I: interruptions s.l., HR_w: heart rate within mean resting heart rate (RHR) ± 2 SD, HR_a: heart rate above RHR ± 2 SD; dur-visit: during human visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; 1 to 4: ranks for proportions calculated during-visit; -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease as compared to during-visit; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase as compared to during-visit; change -1 % to +1 %: values with magnitudes of change lower than ±1 % were excluded from rankings and listed below the table. **N.b.:** If identical proportions appear in rank order, these differed in decimal values. Colour codes follow tab. 5.3.1-6 and tab. 5.3.1-7.

TPT		Decrease Ranks				%dur-visit				Increase Ranks			
		-4	-3	-2	-1	1	2	3	4	+1	+2	+3	+4
R	FAs					Y	$C_{1,2}$	B_1	X	Y	$C_{1,2}$	X	B_1
	%					12	24	24	25	+14	+15	+27	+38
V	FAs	B_1	X	Y	$C_{1,2}$	$C_{1,2}$	X	B_1	Y				
	%	-42	-36	-20	-16	62	64	69	71				
I	FAs	Y	$C_{1,2}$	X		B_1	X	$C_{1,2}$	Y				
	%	-4	-2	-1		3	4	5	7				
HR_w	FAs	C_1				Y	X	B_1	C_1		B_1	Y	X
	%	-3				30	40	41	63		+14	+33	+40
HR_a	FAs	Y	X	B_1	C_1	X	C_1	B_1	Y				
	%	-39	-15	-12	-3	18	30	54	65				

Change -1 % to +1%: Interruptions s.l., FAs-B_1 = -0.73 %

Changes in *total phase number* from pre- to post-visitation: Magnitudes of change calculated for total phase number exceeded ±14 % at FAs-Y for one parameter (HR_above) only. They were lower than that for all other regimes and parameters (tab. 5.3.3-10a).

Patterns in changes of total phase number were no longer readily discernable. A mirrored decrease (excepting FAs-Y, increase) was found with respect to the category 'vigilance' (tab. 5.3.3-10a: V) only. Decreases in the category 'rest' (tab. 5.3.3-10a: R) were observed for FAs-B_1, FAs-Y, and FAs-$C_{1,2}$, while a slight increase in total phase number was seen at FAs-X. Changes in total phase number for the heart rate category 'within' (tab. 5.3.3-10a: HR_w) were next to non-existent for FAs-B_1, and FAs-$C_{1,2}$; proportions decreased for FAs-Y and increased slightly for FAs-X. Changes in total phase number for the category 'interruptions s.l.' (tab. 5.3.3-10a: I), and the heart rate category 'above' (tab. 5.3.3-10a: HR_a) constituted decreases for FAs-X and FAs-Y, and increases for FAs-B_1, and $C_{1,2}$.

In terms of **recovery** (comparing total phase numbers between pre- and post-visitation), it seems noteworthy that irrespective of category, those FAs that had been assigned the highest rank with respect to pre-visit proportions (tab 5.3.3-10a: 4) were invariably found on rank -4 (strongest decrease). For the behaviour, but not the heart rate categories, the opposite pattern also held true, i.e., lowest pre-visit proportions (tab 5.3.3-10a: 1) were increased post-visitation.

Overall propensity to continue to respond in terms of changes in total phase number reflected hypothesised regime differences: It was lowest for FAs-$C_{1,2}$ (sum of absolute magnitudes of response: 14), higher for FAs-X (20) and FAs-B_1 (24), and highest for FAs-Y (33).

Table 5.3.3-10a): Changes from Pre- to Post-Visitation – Ranked Regime Differences in Total Phase Number (TPN) for Selected Behaviour and Heart Rate Categories. Values in **bold red** indicate rank order in concordance with hypothesised differences in severity of regime; values in red suggest conduct-mediated response differences. R: rest, V: vigilance, I: interruptions s.l., HR_w: heart rate within mean resting heart rate (RHR) ± 2 SD, HR_a: heart rate above RHR ± 2 SD; pre-visit: before human visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; 1 to 4: ranks for proportions calculated pre-visit; -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease as compared to pre-visit; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase as compared to pre-visit; change -1 % to +1 %: values with magnitudes of change lower than ±1 % were excluded from rankings and listed below the table. **N.b.:** If identical proportions appear in rank order, these differed in decimal values. Colour codes follow tab. 5.3.1-6 and tab. 5.3.1-7.

TPN		Decrease Ranks				%pre-visit				Increase Ranks			
		-4	-3	-2	-1	1	2	3	4	+1	+2	+3	+4
R	FAs	B_1	Y	$C_{1,2}$		X	Y	$C_{1,2}$	B_1				X
	%	-7	-5	-4		31	31	36	42				+2
V	FAs	B_1	$C_{1,2}$			Y	X	$C_{1,2}$	B_1				Y
	%	-2	-2			37	40	42	44				+6
I	FAs	X				B_1	$C_{1,2}$	Y	X			$C_{1,2}$	B_1
	%	-2				3	8	8	10			+3	+5
HR_w	FAs	Y				C_1	B_1	X	Y				X
	%	-6				46	52	54	55				+3
HR_a	FAs	Y	X			X	C_1	B_1	Y			C_1	B_1
	%	-15	-12			19	29	29	45			+5	+10

Change -1 % to +1%: Vigilance, FAs-X = -0.81 %; Interruptions s.l., FAs-Y = -0.75 %;
HR_w, FAs B_1 = -0.36 %, FAs-C_1 = +0.29 %

Changes in *total phase time* from pre- to post-visitation: Magnitudes of change calculated for total phase time were higher than the respective changes in total phase number (tab. 5.3.3-10b), but considerably less pronounced than those found from pre- to during-visitation (tab. 5.3.3-8b), and slightly less pronounced than from during- to post-visitation (tab. 5.3.3-9b).

Decreases in total phase time of the category 'rest' (tab. 5.3.3-10b: R) were observed in each regime. Unlike total phase number, these decreases tallied with hypothesised graded differences in impact of visiting regime, in that the least pronounced decrease was found for FAs-$C_{1,2}$ (1 P, S&S), and the most pronounced decrease (FAs-Y) corresponded to the visiting regime 3 P, L&F, with FAs-B_1 (1 P, L&F) being assigned to rank -3, and FAs-X (3 P, S&S) occupying rank -2. Excepting FAs-B_1 (next to no change), ranks for increased total phase time for the category 'vigilance' (tab. 5.3.3-10b: V) likewise suggested graded differences in impact of visiting regime: FAs-$C_{1,2}$ exhibited the least pronounced response, followed closely by FAs-X, while FAs-Y received the highest rank. With respect to the heart rate categories, decreased total phase time for the heart rate category 'within' (tab. 5.3.3-10b: HR_w) and increased total phase time for the category 'above' distinguished between visitor conduct rather than number, with higher ranks awarded to 'loud and fast' than to 'silent and slow' visitation. As for the category 'interruptions s.l.', very slight increases (<2 %) remained irrespective of regime.

While all FAs continued to exhibit changes in total phase time, **recovery** was least effected for FAs-Y. *Overall propensity to continue to respond* in terms of changes in total phase time incompletely reflected hypothesised regime differences in that it inverted order for silent and slow regimes: It was lowest for FAs-X (sum of absolute magnitudes of response: 38) and FAs-$C_{1,2}$ (41), higher for FAs-B_1 (62), and highest for FAs-Y (122).

Table 5.3.3-10b): Changes from Pre- to Post-Visitation – Ranked Regime Differences in Total Phase Time (TPT) for Selected Behaviour and Heart Rate Categories. Values in **bold red** indicate rank order in concordance with hypothesised differences in severity of regime; values in red suggest conduct-mediated response differences. R: rest, V: vigilance, I: interruptions s.l., HR_w: heart rate within mean resting heart rate (RHR) ± 2 SD, HR_a: heart rate above RHR ± 2 SD; SD; pre-visit: before human visitation; FA: focal animal, L&F: loud and fast, S&S: silent and slow, 1 P: one visitor, 3 P: three visitors; FAs-B_1: 1 P, L&F; FAs-C_1: 1 P, S&S; FAs-C_2: 3 sessions from 1st day of 1 P, L&F; FAs-X: 3 P, S&S; FAs-Y: 3 P, L&F; 1 to 4: ranks for proportions calculated pre-visit; -4 to -1: ranked magnitude of decrease, whereby -4 = most pronounced decrease as compared to pre-visit; +1 to +4: ranked magnitude of increase, whereby +4 = most pronounced increase as compared to pre-visit; change -1 % to +1 %: values with magnitudes of change lower than ±1 % were excluded from rankings and listed below the table. **N.b.:** If identical proportions appear in rank order, these differed in decimal values. Colour codes follow tab. 5.3.1-6 and tab. 5.3.1-7.

TPT		Decrease Ranks				%pre-visit				Increase Ranks			
		-4	-3	-2	-1	1	2	3	4	+1	+2	+3	+4
R	FAs	**Y**	**X**	**B_1**	**$C_{1,2}$**	$C_{1,2}$	Y	B_1	X				
	%	-42	-18	-7	-6	44	68	69	70				
V	FAs					Y	X	B_1	$C_{1,2}$		$C_{1,2}$	X	Y
	%					17	22	27	45		+2	+7	+34
I	FAs					B_1	Y	X	$C_{1,2}$		Y	B_1	$C_{1,2}$
	%					1	1	2	2		+1	+1	+1
HR_w	FAs	Y	B_1	C_1	X	C_1	B_1	Y	X				
	%	-28	-26	-18	-12	78	81	91	91				
HR_a	FAs					X	Y	C_1	B_1		C_1	Y	B_1
	%					3	9	13	14		+14	+17	+28

Change -1 % to +1%: Vigilance, FAs-B_1 = +0.31 %; Interruptions s.l., FAs-X = +0.64 %; HR_a, FAs-X = -0.12 %

5.3.3.4 Section Summary

N.b.: This section summary will not dwell on regime differences, as these will be presented comprehensively for all sections together in the chapter summary (5.3.4).

This section set out to address the question whether the distribution of phases of behaviour and heart rate as well as posture states observed prior to visitation changed in frequency (phase/ state number) and/or duration (phase/ state time) during and after human visitation. Alterations in ‘flow’ were examined by quantifying between-period differences in distribution (i.e. changes in number of distinct phases/ states, and the time these take up).

5.3.3.4.1 General Between-Period Changes in Phase/ State Distribution

Recapitulation: This analysis was performed to examine overall changes in **‘syntax’** (general between-period changes in flow; i.e., whether phases/ states showed a category-independent tendency to become shorter or longer). ***Total phase/ state number*** and ***time*** were examined irrespective of category for individual duration subclasses (*allCats-indScls*).

To examine general changes, total phase/ state number and total phase/ state time were compared between the periods. Looking at the **pre-visit status quo** (proportions obtained prior to visitation), the short-durations class invariably held the greatest proportion of total phase as well as state numbers, followed – after a large gap – by proportions for the medium- and short-durations classes. In terms of total phase/ state time, proportions were more equally divided between the short- and medium-durations classes with respect to behaviour. For heart rate as well as posture, the long-durations class accounted for more than 50 % of all time. Results (condensed into duration classes, rather than subclasses) are compiled in table 5.3.3-11.

Table 5.3.3-11: Overview of Changes in Total Phase/ State Number and Total Phase/ State Time for All Behaviour, Posture, and Heart Rate Categories before, during, and after Human Visitation. Proportional values are based on total number/ time of phases/ states across all categories per period. For changes, positive values depict increases, negative values represent decreases. TPN: Total Phase Number, TStN: Total State Number, TPT: Total Phase Time, TStT: Total State Time; pre: before human visitation, dur: during human visitation, post: after human visitation; change xx→xy: change from xx to xy; short, medium, long: phase/ state duration classes.

		pre			Change pre→dur			Change dur→post			Change pre→post		
All Categories	**Individual Duration Classes**	**%short**	**%medium**	**%long**	**%short**	**%medium**	**%long**	**%short**	**%medium**	**%long**	**%short**	**%medium**	**%long**
Behaviour	TPN	85.80	12.38	1.82	2.13	-1.48	-0.65	0.84	-0.82	-0.02	**2.96**	**-2.29**	**-0.67**
Posture	TStN	77.17	11.96	10.87	-3.91	14.78	-10.87	-3.65	-9.01	12.66	**-7.56**	**5.77**	**1.79**
Heart Rate	TPN	70.00	20.00	10.00	1.84	-1.84	-0.01	6.69	-1.33	-5.36	**8.53**	**-3.17**	**-5.36**
Behaviour	TPT	41.44	38.73	19.82	6.83	-0.56	-6.27	2.81	-1.69	-1.12	**9.64**	**-2.25**	**-7.39**
Posture	TStT	19.87	19.05	61.08	9.66	51.42	-61.08	-14.28	-49.66	63.94	**-4.62**	**1.76**	**2.86**
Heart Rate	TPT	21.00	25.00	54.00	4.45	1.42	-5.87	8.90	5.36	-14.27	**13.35**	**6.78**	**-20.13**

Behaviour

For all behaviour categories taken together, proportions of total phase number and total phase time assigned to individual duration classes indicated a tendency towards decreases in phase duration from **pre- to during-**, as well as from **during- to post-**visitation: In terms of **recovery** (comparing pre- to post-visitation), the overall increase in phases assigned to the short-durations class amounted to 3 % for phase numbers, and resulted in a 10 % increase with respect to phase time. The corresponding decrease in phase numbers was more pronounced in the medium-durations class, whereas time-wise, the long-durations class was more affected (tab. 5.3.3-11).

Posture

Proportions of total state number and total state time for individual duration classes across both posture categories indicated a trend towards states of medium duration from **pre- to during** visitation: Despite a 4 % loss in total state number, the short-durations class gained 10 % in total state time, suggesting within-class shifts towards longer subclasses (i.e. ‘approaching’ the medium-durations class). The medium-durations class increased in both numbers and time. In contrast, the long-durations class disappeared entirely[31]. From **during- to post-**visitation, a trend towards longer state durations was found: The short-durations class decreased below pre-visit proportions, the medium durations-class returned to slightly above pre-visit levels, and the long-durations class was ‘reinstated’ beyond pre-visit proportions (tab. 5.3.3-11). In terms of **recovery** (comparing pre- to post-visitation), the overall change consisted of decreases in the short-durations class and slight increases in the medium- and long-durations classes so that the pattern was distinctly different from pre-visitation.

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[31] pre-value = 61.08 %, change-value pre→dur = -61.08 %, resulting in 0 % during-visitation

Heart Rate

Proportions of total phase number and total phase time for individual duration classes across all heart rate categories indicated a tendency towards decreases in phase duration from **pre- to during-**, as well as from **during- to post-**visitation. In terms of **recovery** (comparing pre- to post-visitation), the pattern was distinctly different from pre-visitation: The overall increase in phases assigned to the short-durations class amounted to 9 % in terms of phase numbers, and resulted in a 13 % increase with respect to phase time. The corresponding decrease in phase numbers was found in the medium- as well as in the long-durations class, whereas time-wise, only the long-durations class decreased, while the medium-and short-durations classes increased (tab. 5.3.3-11). Between-period changes in total phase time thus resulted in an increasing **equalisation** of proportions of time allotted to the different duration classes.

5.3.3.4.2 Between-Category Changes in Phase/ State Distribution

Recapitulation: This analysis was performed to gain an insight into the **composition** of behaviour/ posture/ heart rate (between-period changes among the categories examined) with respect to ***total phase number*** and ***time***, i.e., irrespective of duration classes (*indCats-allScls*).

Looking at the **pre-visit status quo** (tab. 5.3.3-12), the proportional composition of behaviour was dominated by phases of ‘rest’ (total phase number: 36 %, total phase time: 62 %) and ‘vigilance’ (total phase number: 42 %, total phase time: 29 %). Results (condensed into duration classes, rather than subclasses) are compiled in table 5.3.3-12.

Proportions for the two postures were approximately equal in terms of phase number (52 %, and 48 %, for ‘prone’ and ‘up’, resp.), while time-wise, ‘prone’ states outweighed ‘up’ states by far (83 %, and 17 %, resp.).

As for heart rate, the category ‘within’ held the greatest proportion of phases in terms of both number (51 %) and time (85 %).

Behaviour

From **pre- to during-visitation** (tab. 5.3.3-12), examination of proportions of total phase number and total phase time for each behaviour category for all duration classes together (in log-diagrams: ‘bricked’ logs), revealed marked decreases in number (-10 %) and time (-40 %) of resting phases. Additionally, slight decreases were found in comfort behaviour, whereas the other four behaviour categories increased[32]. Of these, the increase in vigilance behaviour was slight with respect to phase number (+1 %), but most pronounced in terms of time taken up (+37 %). Phase number (+7 %) as well as phase time (+3 %) of ‘interruptions s.l.’ nearly doubled.

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[32] With respect to the category ‘breed’, a slight increase in phase number effected an even slighter increase in phase time.

From **during- to post-visitation**, responses in both number and time generally 'counteracted' those observed from pre- to during-visitation (increases followed by decreases and vice versa), except for the category 'breed', which 'continued' to increase.

Recovery (comparing pre- to post-visit proportions) was most notably incomplete with respect to resting behaviour (-3 % in number, and -13 % in time) and also for breeding behaviour (+3 % in number, +4 % in time). In the category 'vigilance', phase time (+6 %), but not number remained elevated.

Posture

From **pre- to during-visitation** (tab. 5.3.3-12), examination of proportions of total state number and total state time for each posture category for all duration classes together (in log-diagrams: 'bricked' logs), revealed marked decreases in 'prone' states (-14 % in state number, -42 % in state time) and corresponding increases in 'up' states.

From **during- to post-visitation**, responses were reversed but failed to entirely re-establish pre-visit proportions. **Recovery** (comparing pre- to post-visit proportions), nevertheless, was considered approximately complete (remaining deviations: -2 % 'prone' states, +2 % 'up' states).

Table 5.3.3-12: Overview of Changes in Total Phase/ State Number and Total Phase/ State Time for Individual Behaviour, Posture, and Heart Rate Categories before, during, and after Human Visitation. Proportional values are based on total number/ time of phases/ states across all categories per period. For changes, positive values depict increases, negative values represent decreases. interruptions s.l.: within-phase interruptions, between-phase interruptions, transitionary phases, and 'headshake-phases'; below, within, above: categories based on resting heart rate ±2SD; TPN: Total Phase Number, TStN: Total State Number, TPT: Total Phase Time, TStT: Total State Time; pre: status quo before human visitation, dur: during human visitation, post: after human visitation; change xx→xy: change from xx to xy; short, medium, long: phase/ state duration classes.

All Duration Classes **Individual Categories**			**pre**	**Change pre→dur**	**Change dur→post**	**Change pre→post**
Behaviour	rest	TPN	36.25	-10.45	7.07	**-3.38**
	comfort		3.22	-0.82	0.54	**-0.28**
	breed		6.92	0.93	1.91	**2.84**
	vigilance		41.68	1.21	-2.05	**-0.84**
	agonistics		4.97	2.43	-2.49	**-0.06**
	interruptions s.l.		7.06	6.70	-4.98	**1.72**
Posture	prone	TStN	52.17	-13.56	11.39	**-2.17**
	up		47.83	13.56	-11.39	**2.17**
Heart Rate	below	TPN	19.58	-0.23	-0.89	**-1.12**
	within		51.05	-5.89	5.10	**-0.79**
	above		29.37	6.11	-4.20	**1.91**
Behaviour	rest	TPT	62.28	-39.71	26.84	**-12.87**
	comfort		2.89	-1.56	2.44	**0.88**
	breed		2.72	0.31	3.72	**4.03**
	vigilance		28.96	37.27	-30.97	**6.30**
	agonistics		1.53	1.01	-0.50	**0.51**
	interruptions s.l.		1.62	2.67	-1.51	**1.16**
Posture	prone	TStT	83.42	-42.08	41.27	**-0.81**
	up		16.58	42.08	-41.27	**0.81**
Heart Rate	below	TPT	5.17	9.36	-5.80	**3.56**
	within		85.20	-42.18	18.12	**-24.06**
	above		9.63	32.82	-12.33	**20.49**

Heart Rate

From **pre- to during-visitation** (tab. 5.3.3-12), examination of proportions of total phase number and total phase time for each heart rate category for all duration classes together (in log-diagrams: 'bricked' logs), revealed little change in numbers for the category 'below', decreases in the category 'within', and increases in the category 'above'. Time-wise, the category 'below' almost tripled (+9 %), the category 'above' increased markedly (+33 %), while the category 'within' decreased correspondingly.

From **during- to post-visitation**, responses were reversed but failed to completely re-establish pre-visitation levels. **Recovery** (comparing pre- to post-visit proportions) was approximately complete with respect to total phase number (remaining deviations below 2 %), but notably incomplete with respect to total phase time, with 20 % more phase time accounted for by the category 'above' and -24 % phase time assigned to the category 'within'.

5.3.3.4.3 Within-Category Changes in Phase/ State Distribution

Recapitulation: This analysis was performed to examine within-category changes in **'syntax'**, i.e. in ***category phase/ state number*** and ***time*** during and after visitation (*indCats-indScls*).

Looking at the **pre-visit status quo** (tab. 5.3.3-13), proportions of category phase/ state number predominantly fell into the short-durations class for all parameters, with the parameter heart rate – within' being the only one to exhibit approximately equal proportions for short- and medium-durations classes. Results (condensed into duration classes, rather than subclasses) are compiled in table 5.3.3-13.

With respect to category phase/ state time, most parameters likewise predominantly 'occupied' the short-durations class, with approximately equal proportions in the short- and medium-durations class found for the parameter behaviour – 'comfort' only. Maximum proportion for the parameter behaviour – 'rest' was assigned to the medium-durations class, while maximum proportions for the parameters posture – 'prone' as well as heart rate – 'within' fell into the long-durations class.

Behaviour

Looking at changes in individual duration classes for each behaviour category (tab. 5.3.3-13), phase duration from **pre- to during-**visitation was reduced with respect to the categories 'rest', 'comfort', 'breed', and 'agonistics' (for the latter, within-class shift towards shorter phases), whereas an increase in phase durations was found for the categories 'vigilance' and 'interruptions s.l.' (for the latter, within-class shift towards longer phases).

Changes from **during- to post-**visitation generally counteracted the changes described above.

Failure to achieve complete recovery was found in several categories: With respect to phases of resting behaviour, the short-durations class gained in both number (7 %) and time (8 %). A greater proportion (comparing post- to pre-visit proportions) of both phase number (4 %) and time (15 %) of breeding behaviour was assigned to the medium-durations class. While only a slight change was found in phase number of agonistic behaviour, phase time accounted for by the medium-durations class was augmented by 6 %.

With respect to comfort behaviour, within-class shifts towards longer phase durations occurred in both the short- and medium-durations classes. Similar within-class shifts (short-durations class only) were found for the category 'interruptions s.l.'.

Table 5.3.3-13: Overview Changes in Category Phase/ State Number and Category Phase/ State Time for Individual Behaviour, Posture, and Heart Rate Categories before, during, and after Human Visitation. Proportional values are based on total number/ time of phases/ states per category per period. For changes, positive values depict increases, negative values represent decreases. R: rest, C: comfort, B: breed, V: vigilance, A: agonistics, I: interruptions s.l. comprising within-phase interruptions, between-phase interruptions, transitionary phases, and 'headshake-phases'; P: posture prone, U: posture up; b, w, a: heart rate categories below, within, and above, based on resting heart rate ±2SD; $0.00^{\#}$: within-class changes occurred; CPN: Category Phase Number, CStN: Category State Number, CPT: Category Phase Time, CStT: Category State Time; pre: status quo before human visitation, dur: during human visitation, post: after human visitation; change xx→xy: change from xx to xy; short, medium, long: phase/ state duration classes.

Individual Duration Classes / Individual Categories			pre			Change pre→dur			Change dur→post			Change pre→post		
			%short	%medium	%long	%short	%medium	%long	%short	%medium	%long	%short	%medium	%long
Behaviour	R	CPN	72.15	23.02	4.48	17.75	-13.67	-4.08	-10.36	7.96	2.40	**7.39**	**-5.71**	**-1.68**
	C		84.78	15.22	0.00	9.81	-9.81	0.00	-11.26	11.26	0.00	**-1.45**	**1.45**	**0.00**
	B		97.98	2.02	0.00	1.19	-1.19	0.00	-4.76	4.76	0.00	**-3.57**	**3.57**	**0.00**
	V		91.61	8.22	0.17	-13.24	11.14	2.10	13.22	-11.22	-2.00	**-0.02**	**-0.08**	**0.10**
	A		100.0	0.00	0.00	$0.00^{\#}$	0.00	0.00	-1.11	1.11	0.00	**-1.11**	**1.11**	**0.00**
	I		100.0	0.00	0.00	$0.00^{\#}$	0.00	0.00	$0.00^{\#}$	0.00	0.00	**0.00**	**0.00**	**0.00**
Posture	P	CStN	64.58	14.58	20.83	7.21	13.62	-20.83	-18.63	-6.69	25.32	**-11.42**	**6.93**	**4.49**
	U		90.91	9.09	0.00	-16.72	16.72	0.00	11.88	-11.88	0.00	**-4.84**	**4.84**	**0.00**
Heart Rate	b	CPN	96.43	3.57	0.00	-13.10	8.93	4.17	11.11	-6.94	-4.17	**-1.98**	**1.98**	**0.00**
	w		43.84	36.99	19.18	20.45	-8.41	-12.04	4.08	-4.08	0.00	**24.53**	**-12.50**	**-12.50**
	a		97.62	0.00	2.38	-22.62	6.82	15.80	10.25	3.02	-13.26	**-12.37**	**9.84**	**2.54**
Behaviour	R	CPT	25.08	44.22	30.70	30.85	-9.05	-21.80	-22.94	9.05	13.89	**7.91**	**0.00**	**-7.91**
	C		54.02	45.98	0.00	24.64	-24.64	0.00	-26.14	26.14	0.00	**-1.50**	**1.50**	**0.00**
	B		90.46	9.54	0.00	4.78	-4.78	0.00	-19.33	19.33	0.00	**-14.55**	**14.55**	**0.00**
	V		64.42	33.15	2.43	-26.86	11.87	14.99	27.64	-13.54	-14.10	**0.78**	**-1.67**	**0.89**
	A		100.0	0.00	0.00	$0.00^{\#}$	0.00	0.00	-5.92	5.92	0.00	**-5.92**	**5.92**	**0.00**
	I		100.0	0.00	0.00	$0.00^{\#}$	0.00	0.00	$0.00^{\#}$	0.00	0.00	**0.00**	**0.00**	**0.00**
Posture	P	CStT	12.03	14.75	73.22	14.16	59.06	-73.22	-18.16	-59.24	77.40	**-4.00**	**-0.18**	**4.18**
	U		59.33	40.67	0.00	-27.44	27.44	0.00	17.70	-17.70	0.00	**-9.74**	**9.74**	**0.00**
Heart Rate	b	CPT	88.89	11.11	0.00	-51.23	18.76	32.47	41.65	-9.18	-32.47	**-9.58**	**9.58**	**0.00**
	w		10.29	28.67	61.05	12.96	16.51	-29.47	3.36	-6.51	3.15	**16.31**	**10.00**	**-26.32**
	a		77.61	0.00	22.39	-54.50	6.22	48.28	13.39	14.78	-28.17	**-41.11**	**21.00**	**20.11**

Posture

As for changes in posture (tab. 5.3.3-13) from **pre- to during**-visitation, 'prone' states were reduced in duration with respect to both number and time (less states assigned to the long-durations-class, more states falling in the short- and medium-durations classes), while duration of 'up' states increased, and more states fell into the medium-durations class.

Changes from **during- to post-**visitation counteracted those found before: In terms of **recovery**, fewer states of both postures were assigned to the short-durations class after than prior to visitation so that the pattern was distinct from that encountered prior to visitation.

Heart Rate

The three heart rate categories underwent a notable change from **pre- to during-**visitation (tab. 5.3.3-13): In the category ‘below’ a greater proportion of phase number as well as time was assigned to the medium- and long-durations classes (with the latter not having been ‘occupied’ prior to visitation). In the category ‘within’, a greater proportion of phase number as well as time fell into the short-durations class, with corresponding losses found in the long-durations class. The medium-durations class was reduced in terms of phase number, but increased in terms of phase time. In the category ‘above’, the short-durations class received a lesser proportion of phase number as well as time, while a greater proportion was assigned to the (previously unoccupied) medium-durations class, and particularly to the long-durations class.

From **during- to post-**visitation, changes counteracted those described above, but generally failed to result in a complete **recovery**: In the category ‘below’, proportion of phase number recovered almost completely (to within 2 %), but a greater proportion of time was accounted for by phases assigned to the medium-durations class, suggesting longer phase durations in this category. Phase duration was shorter in the category ‘within’, and longer in the category ‘above’.

5.3.3.4.4 Further Findings – ‘Impurities’ and Posture Changes

As for the behaviour parameter **‘impurities’**, proportion of within-phase impurities increased **during visitation** and decreased again **after visitation**, but remained higher than pre-visit so that **recovery** was incomplete. Proportion of between-phase impurities did not markedly change between periods.

Frequency of posture changes was analysed by Friedman-test. The test indicated a highly significant difference between periods (c^2=13.000, *p*=0.002, n=51), caused by differences between pre- and during-visit rates (c^2=15.158, *p*=0.000, n=51). Frequency of posture changes increased **during** visitation, but the decrease after visitation **‘recovered’** to approximately pre-visit level.

During visitation, frequency of posture changes was greatest at the visiting stage ‘visitor at 5 m’, followed by the stage ‘visitor at 3 m’, and least pronounced at the stage ‘visitor at 15 m’.

5.3.3.4.5 Comprehensive Overview on Post-Visit Recovery

Behaviour

The **overall pattern** of behaviour phases (‘syntax’ of behaviour, distribution of phase durations across the duration classes irrespective of category) underwent a slight shift towards shorter phase durations (tab. 5.3.3-11). The **composition** of behaviour (proportions taken by each behaviour category) was distinctly altered **during** visitation, and the change was not entirely reversed **after** visitation had ended. In terms of **recovery** (comparing pre- to post-visit), changes in phase number were comparatively small, but more time was devoted to vigilance and breeding behaviour, and less time to resting behaviour so that recovery must be termed incomplete (tab. 5.3.3-12). Within **individual categories** (‘within-parameter syntax’; tab. 5.3.3-13), shorter phase durations were found in the category ‘rest’, while longer phase durations were noted in the categories ‘comfort’, ‘breed’, ‘agonistics’, and ‘interruptions s.l.’. Vigilance behaviour was thus the only behaviour for which no changes in phase duration persisted beyond the actual visitation period (post-visit: ‘more’, but not differently distributed).

Posture

The **overall pattern** of posture state durations ('syntax') changed towards longer durations and appears to have been affected by human visitation (tab. 5.3.3-11). The **composition** of posture (distribution of states between categories) changed **during** visitation. Up states became more frequent in both state number and time, but distributions **pre- and post-**visitation were almost indistinguishable, pointing to complete **recovery** (tab. 5.3.3-12). Within **individual categories** ('within-parameter syntax'; tab. 5.3.3-13), changes towards longer states were found for both categories.

Heart Rate

The **overall pattern** of heart rate phases ('syntax') changed towards shorter phase durations and is suggested to have been affected by human visitation (tab. 5.3.3-11). The **composition** of heart rate (distribution of phases among the three categories) changed **during** visitation, with more phases assigned to the category 'above' and less to the category 'within'. **After** visitation, proportions of phase number were almost indistinguishable from pre-visitation proportions, while proportions of phase time remained elevated for the category 'above' and depressed for the category 'within' so that **recovery** must be considered incomplete (tab. 5.3.3-12). Within **individual categories** ('within-parameter syntax'; tab. 5.3.3-13), changes towards longer phases occurred in the categories 'below' and – more prominently – 'above', while shorter phases were found in the category 'within'.

5.3.4 Chapter Summary

Changes in behavioural, postural, and heart rate **topography** were examined on **three levels**. Each level aimed at answering a specific **key question**.

Visual Appraisal addressed the question of consistency of changes across focal animals both qualitatively ('graphical' examination) and quantitatively (tabulated proportions of sessions during which responses were obtained). The **key question** to be answered was 'How many?'

Quantitative Comparison of Prevalence of behaviour systems and postures examined the magnitude of changes in behaviour and posture before, during, and after human visitation. Additionally, the magnitude of heart rate variation was analysed using a set of 8 (descriptive) statistical parameters. The **key question** asked was 'How much?'

3. Distribution of Phase/ State Durations before, during, and after human visitation examined structural and compositional alterations in 'flow', by quantifying changes in the duration of behaviour and heart rate phases and posture states. The **key question** of this section thus asked 'In what way?'

5.3.4.1 Visual Appraisal

Visual appraisal was undertaken for a total of 9 comportment parameters, comprising 7 **behavioural** parameters (scattered behaviour, resting, comfort, breeding, vigilance, agonistics, and occurrence of headshakes), as well as **posture changes** and **heart rate**.

Consistency of responses was reflected in the proportion of sessions (n=51) a given response was obtained. Visual appraisal assessed impact of **non-human disturbance** (conspecifics and to a lesser extent of skua and aircraft) outside human visitation, and examined between-period changes in comportment before (five consecutive 2 min-intervals), during (each visiting stage) and after **human visitation** (five consecutive 2 min-intervals).

Non-Human Disturbance**:** None of the comportment parameters changed detectably in response to **conspecific 'stationary' presence** at the focal nest.

As regards **conspecific movement**, visual appraisal indicated a graded response with respect to some behavioural parameters, but not heart rate: Conspecific **movement irrespective of distance** to the focal nest frequently elicited increased vigilance, increased scattering of behaviour (several behaviour systems displayed in short succession) and decreased resting, but rarely resulted in increased agonistic behaviour. This, in turn, was most often observed in response to conspecific **movement at the focal nest**. Heart rate changes in response to conspecifics were very rarely observed and only coincided with general movement, but not with movement at the focal nest so that a graded response must be discounted for this parameter. The remaining parameters did not constitute indicators for conspecific movement. In terms of ***gradation of response***, general conspecific movement is suggested to be perceived as less threatening to FAs – thereby drawing a vigilance response with vigilance behaviour 'replacing' resting behaviour. Movement close to the focal nest, in contrast, incurs the risk of nest stone theft or direct aggression, and elicits a more forceful response (agonistic behaviour). Since agonistic behaviours rarely take up longer stretches of time, 'replacement' of resting behaviour does not necessarily become apparent.

Despite their rarity, occurrences of **predator** and **aircraft** disturbance likewise suggested a graded response for the former, in that **skua** low overflights often coincided with decreased resting and increased vigilance behaviour, while skua presence on the ground almost invariably elicited these responses and additionally led to increased agonistic behaviour. In terms of ***gradation of response***, skua low overflights (further away) cause a stronger response in vigilance behaviour, while during skua presence on ground (closer) agonistic responses are added. Skua presence on the ground elicited a heart rate response in 1 of a total of 3 sessions; no heart rate reactions were found with respect to skua low overflights (0 of 8 sessions). **Aircraft** noise 'always'[33] resulted in increased vigilance, but not increased agonistic or decreased resting behaviour. In the only session during which (legible) heart rate recording and aircraft presence coincided, no response was obtained.

Human Visitation**:** In contrast to responses towards conspecifics and predator/ aircraft disturbance, **human visitation** led to alterations in all comportment parameters analysed: Increases were found with respect to the parameters heart rate, posture changes, and for all behavioural parameters except resting behaviour (distinct decrease) and comfort behaviour (ambiguous changes, both increases and decreases).

Human visitation thus caused focal animals to substantially alter their overall comportment **during** the visit itself. Maximum response consistency (in 80 % to 85 % of all sessions examined) was found as regards decreased resting, increased vigilance behaviour and increased heart rate, while increased scattering was observed in approximately half of all sessions. Additionally, increases in occurrence of headshakes, posture changes, breeding and agonistic behaviour were found in more than a third of all sessions.

Antidirectional changes (examined per visiting stage for all FAs together), predominantly grouped decreased resting with increased vigilance and increased heart rate (from 'visitor approach to 15 m' up to and including 'visitor retreat'). Decreased resting behaviour was additionally frequently accompanied by increased agonistic and breeding behaviour (from 'visitor at 15 m' up to and including 'visitor retreat'). Syndirectional changes mainly concerned increased vigilance in conjunction with increased heart rate, occurrence of headshakes, posture changes, and agonistics (from 'visitor approach to 15 m' up to and including 'visitor retreat'). From the stage 'visitor at 15 m'

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[33] 'Always' comprising three sessions, no predictions as to representativity are ventured.

onwards, increased vigilance was additionally frequently accompanied by increased breeding behaviour.

The **visiting stages** from and including ‘visitor approach to 5 m’ to and including ‘visitor stay at 3 m’ encompassed the greatest changes in most comportment parameters. Focal-animal heart rate, however, was more sensitive to stimuli moving towards the birds than to stimuli remaining at a stable distance, with highest proportional value for increased heart rate assigned to the stage of ‘visitor approach to 5 m’, and second highest value to the stage of approach to 3 m. As observed with respect to conspecific movement and tentatively assumed as regards skuas, a ***graded response*** towards human visitation at different distances from the focal nest was found for the parameters vigilance and agonistics.

Furthermore, findings suggest that focal-animal responses tended to persist well **beyond the end** of human visitation. Compared to during-visit, however, a waning of responses resulted in substantially (heart rate, rest, vigilance) to considerably (scattering, posture changes, agonistics) lower maximum response consistency observed. While for these parameters a ‘continuing return’ towards pre-visit levels seemed likely – albeit not completely effected at the end of the post-visit period –, maximum values calculated for occurrence of headshakes as well as for behaviours of nest or self maintenance (i.e. breeding and comfort behaviour) remained unchanged or even increased.

Antidirectional changes (examined per post-visit interval for all FAs together) predominantly grouped decreased resting with increased vigilance, but the opposite conjunction became increasingly more common during the post visit-period. Decreased resting behaviour additionally frequently coincided with increased breeding, and to a lesser extent, with increased agonistic behaviour and heart rate. Syndirectional changes mainly concerned increased vigilance in conjunction with increased occurrence of headshakes, breeding, posture changes, and – to a much lesser extent with increased agonistics and increased heart rate.

The first three of the five **post-visit intervals** contained the greatest changes in comportment, but unlike during visitation, parameters were far more different in pattern. Resting behaviour was the only comportment parameter to exhibit a successive waning of response (less decrease), whereas increased scattered behaviour and vigilance peaked in the second, and increased breeding and comfort behaviour as well as posture changes peaked in the third post-visit interval. With respect to increased occurrence of headshakes and increased agonistic behaviour, the downward tendency for overall response levels exhibited slight fluctuations. The pattern for increased heart rate was unusual (second highest value in fourth post-visit interval).

For all of the comportment parameters examined these findings indicate a **relative recovery** within the post-visit period, but suggest that at least for some birds, this time (10 min) was not sufficient to recuperate and return to the comportment exhibited prior to visitation.

5.3.4.2 Quantitative Comparisons

Quantitative comparison of **prevalence** of was undertaken for a total of 7 parameters, comprising 6 behavioural parameters (resting, comfort, breeding, vigilance, agonistics, and headshakes) and the posture ‘prone’. Prevalence in heart rate being unquestionable, the extent of heart rate **variation** in ‘visited’ as well as ‘baseline’ sessions (no human interference) was analysed using a total of 8 statistical parameters (mean, SD, minimum, 1st quartile, median, 3rd quartile, maximum, and range).

Quantitative comparisons assessed the between-period **magnitude of changes** in **prevalence** of behaviour and posture **irrespective of** their **underlying structure** (distribution of phases, states). The same applied to heart rate (variation, but not distribution of phases). Examination of 'baseline' sessions additionally permitted comparison of extent of between-period variation in heart rate found for sessions including human visitation with variation observed in sessions in which no visit had occurred.

Quantitative comparisons demonstrated that **during human visitation**, behaviour (particularly resting and vigilance, as well as headshakes), posture ('prone'), and a number of heart rate statistical parameters (particularly maximum, range, and standard deviation) were significantly different from pre-visitation levels. Moreover, the cessation of human presence did not generally result in complete **recovery after visitation**.

With respect to heart rate statistical parameters, the **comparison of visited and 'baseline'** sessions additionally showed that increases found during visitation were not paralleled by increases in the corresponding 2nd 10 min-interval of unvisited sessions, indicating heart rate responses to human visitation to markedly exceed naturally occurring fluctuations.

As quantitative comparisons of prevalence in behaviour and posture looked at individual sessions as well as analysing similarity of behaviour/ posture across sessions, a high degree of intra- and inter-animal **individuality** became apparent, particularly with respect to comfort, breeding, and agonistic behaviours.

For all behaviour parameters examined as well as for posture, **incomplete recovery** (returning towards, but not reaching pre-visit levels) or **'overshooting'** (returning towards and going beyond pre-visit levels) were frequently observed during the post-visit period. The magnitude of differences in response between pre- and post-visit found in individual sessions was extremely variable. With respect to **recovery**, the range of between-period differences (span from min. to max.) was substantial for all parameters, pointing to the persisting individuality of behavioural and postural post-stimulus responses and, ultimately, recovery.

5.3.4.3 Distribution of Behaviour and Heart Rate Phases and Posture States

Distribution of Phases and States examined **structural and compositional alterations** in 'flow' by quantifying changes in the frequency (phase/ state number) and duration (phase/ state time) of behaviour phases (6 categories: 'rest', 'comfort', 'breed', 'vigilance', 'agonistic behaviour' and 'interruptions[34] s.l.'), posture states (2 categories: 'prone' and 'up'), and heart rate phases (3 categories: 'below', 'within', and 'above' resting heart rate ±2 SD).

Recapitulation: The term 'structural alterations' refers to changes in the **'syntax'** of comportment which may concern all categories (e.g., more and overall shorter behaviour phases) or specific categories (e.g., more and longer states of posture 'up'). Depending on interplay of number and time of phases/ states, structural alterations will or will not cause changes in the **composition** of comportment (i.e., more resting phases need not result in more time spent resting, if long resting phases disappear and short resting phases do not increase dramatically).

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[34] of which headshakes (incl. ruffle-shakes) are frequent components

In a first step, the overall distribution of phases/ states in the short-, medium- and long-durations classes was examined irrespective of category for ***total phase/ state number*** and ***time*** (*allCats-indScls*). Human visitation altered the **‘syntax’** of behaviour, posture, and heart rate. Changes were observed from **pre- to during-** as well as from **during- to post-**visitation. The latter did not result in a return to pre-visit conditions and thus **recovery**.

With respect to behaviour phases, total phase number and total phase time exhibited a tendency towards decreases in phase duration from **pre- to during-**, as well as from **during- to post-**visitation, whereby more phases were assigned to the short-durations class.

As regards posture states, total state number and time showed a trend towards medium-durations from **pre- to during-**visitation (with the long-durations class disappearing entirely), substituted by a trend towards longer durations from **during- to post-**visitation (with the long-durations class reinstated beyond pre-visit proportions).

Distribution of heart rate phases indicated a tendency towards decreases in phase duration from **pre- to during-**, as well as from **during- to post-**visitation as regards both total phase number and time. With respect to total phase time, between-period changes resulted in an increasing equalisation of proportions of time allotted to the different duration classes.

In the next step, the distribution of phases/ states was examined separately for each behaviour, posture, and heart rate category but irrespective of duration subclasses (*indCats-allScls*).

From **pre- to during-visitation**, ***total phase/ state number*** and ***total phase/ state time*** were substantially altered for the majority of parameters, leading to marked changes in the overall **composition** of behaviour, posture, and heart rate.

A distinctdecrease in both number and time (‘less often and shorter’) was found with respect to resting phases, posture ‘prone’ and the heart rate category ‘within’. Additionally, there was a slight decrease in comfort behaviour. This was accompanied by a pronounced increase in phase time, but not number (‘not more often, but longer’) of vigilance phases, and heart rate phases assigned to the category ‘below’, while a small increase in phase number effected a very slight increase in phase time (‘more often, but not much longer’) with respect to the category ‘breed’. An increase in both number and time (‘more often and longer’) occurred as regards the categories ‘interruptions s.l.’, posture ‘up’, and ‘heart rate – above’.

From **during- to post-visitation**, responses generally ‘counteracted’ those observed from pre- to during-visitation, but – equally generally – failed to re-establish pre-visit levels. The category ‘breed’, which exhibited a distinct further increase, represented a notable exception from this rule.

Recovery (comparing pre- to post-visit proportions of total phase/ state number and time per category) was most notably incomplete with respect to resting behaviour, which remained decreased, and also for breeding behaviour, which continued to increase. In the category ‘vigilance’, phase time, but not number remained elevated. Recovery was more or less complete as regards posture. As for heart rate, recovery was approximately complete in terms of total phase number, but notably incomplete with respect to phase time, with 20 % more phases assigned to the category ‘above’ and 24 % less to the category ‘within’.

Finally, the distribution of phases/ states among the duration subclasses was examined for each behaviour, posture, and heart rate category (*indCats-indScls*).

From **pre- to during-visitation**, changes in ***category phase/ state number*** and ***category phase/ state time*** were found for the majority of parameters. Different directions of changes in different parameters to some degree explain the moderate extent of overall changes in ‘syntax’ of comportment.

A marked **shift** towards the **short-durations class** in both number and time was found with respect to phases of resting, comfort, breeding, posture ‘prone’, and the heart rate category ‘within’. Additionally, phases of agonistic behaviour underwent a within-class shift towards shorter durations (indicating a change from defensive to offensive agonistic behaviour elements, as the latter take up considerably less time).

This was complemented by a pronounced **shift** towards **longer duration classes** in the behaviour category ‘vigilance’, the posture category ‘up’, and heart rate phases assigned to the categories ‘below’ and ‘above’. As for the category ‘interruptions s.l.’, a within-class shift towards longer durations was observed.

From **during- to post-visitation**, responses generally ‘counteracted’ those observed from pre- to during-visitation, but – equally generally – failed to re-establish pre-visit levels.

Recovery (comparing pre- to post-visit proportions of total phase/ state number and time per category) was not achieved for a number of categories. A **persisting shift** towards **shorter phase durations** was observed with respect to resting behaviour and the heart rate category ‘within’.

A **shift** towards **longer duration classes**, in contrast, was found for breeding behaviour and the heart rate category ‘above’. Within-class shifts towards longer phase durations were additionally registered for the behaviour categories of ‘comfort’, ‘agonistics’, and ‘interruptions s.l.’ as well as for the heart rate category ‘below’. As for posture, fewer states of both posture categories were assigned to the short-durations class after than prior to visitation so that the pattern was distinct from that encountered prior to visitation.

In the category ‘vigilance’, proportions assigned to each duration class were approximately indistinguishable from distribution found prior to visitation, i.e., while the level of vigilance behaviour remained augmented – cf. total phase time – the structure had returned to that observed pre-visit.

Further findings included an increase in within-phase ‘impurities’ (but not before-phase ‘impurities’) during- and after visitation, and an elevation of occurrence of posture changes during, but not after visitation.

5.3.4.4 Regime Differences

All sections above had examined responses irrespective of visiting regime (across all focal animals = FAs) as well as looking for regime-specificity of changes observed (graded response to regimes hypothesised to differ in severity of impact). Here, a comprehensive overview on regime differences detected by the various analyses is provided.

Responses of focal animals subjected to different visiting regimes were ranked, and the rank orders obtained were used to identify response patterns. Apart from response gradients tallying with hypothesised severity of regime (see recapitulation below), conduct-mediated (loud and fast vs. silent and slow) as well as animal-dependent patterns became apparent.

Recapitulation: In terms of severity, loud and fast visitation is hypothesised to exceed impact of silent and slow visitation, while 3 visitors are assumed to exert a greater impact than 1 visitor. Ranking the regimes employed in this study, the following order would ensue:

3 P, L&F (FAs-Y) > 1 P, L&F (FAs-B_1; FAs-C_2) $\geq$ 3 P, S&S (FAs-X) > 1 P, S&S (FAs-C_1)

N.b.: In the text, FAs-$C_{1,2}$ will be summarily referred to as having been subjected to 'predominantly the regime 1 P, S&S', as next to no difference in comportment had been observed in the first session following the switch in regimes (to 1 P, L&F).

5.3.4.4.1 Regime Differences as Detected by Visual Appraisal

Regime differences were examined with respect to the **proportion of birds responding** to human visitation during a given visiting stage/ post-visit interval (How many?). Visual appraisal emphasised the utility of looking at several comportment parameters conjointly rather than solely at isolated parameters: Graded responses were observed in each visiting stage (except 'visitor approach to 3 m'; lasting only a couple of seconds) and each post-visit interval, but gradation was never found for all parameters together.

For increased scattering, regime-graded responses during visitation were encountered in the visiting stages 'visitor at 15 m', 'visitor at 5 m', and during visitor retreat. Post-visit, they were found during the fourth post-visit interval (7-8 min); additionally, ranked responses tallied with visitor conduct during the fifth post-visit interval (9-10 min).

As for decreased resting behaviour, conduct-graded responses were observed in the first two visiting stages (approach to and stay at 15 m) during visitation, while regime-graded responses after visitation occurred in the third (5-6 min) and fifth (9-10 min) post-visit interval.

Graded responses with respect to the comportment parameter 'breed' (increase) appeared linked to withdrawal of disturbance stimulus; they occurred during visitor retreat (regime-graded) and the first post-visit interval (conduct-graded) after visitation.

As regards increased vigilance, regime-graded responses were found in the first two visiting stages (approach and stay at 15 m) and during visitor stay at 3 m, as well as during the first (1-2 min), second (3-4 min), and fifth post-visit intervals.

Increased occurrence of headshakes tallied with hypothesised severity of regime during visitor approach to 5 m only.

Concerning increased occurrence of posture changes, a regime-graded response was found during visitor approach to 15 m, while response during visitor stay at 5 m was conduct-mediated. After visitation, a conduct-graded response was found during the first post-visit interval, while responses observed in the second and fifth post-visit intervals tallied with hypothesised regime differences.

Graded responses in the parameter 'heart rate' (increase) were frequently encountered during visitation (approaches to 15 m and 5 m, stay at 3 m, retreat; all regime-mediated) as well as in the first (regime-mediated), fourth (conduct-mediated), and fifth (regime-mediated) post-visit intervals.

While **mean values** during visitation revealed a regime-graded response for heart rate only, mean post-visit values reflected a conduct-graded response with respect to increased scattering, and regime-graded responses as regards decreased rest, increased vigilance and increased posture changes.

Addition of rank positions encountered at each visiting stage and each post-visit interval revealed an overall greater number of most pronounced responses for FAs-Y (3 P, L&F), complemented by an overall greater number of least pronounced responses for FAs-$C_{1,2}$ (mainly 1 P, S&S). During visitation, FAs-Y were most frequently encountered on ranks ±4 (most pronounced response), FAs-B_1 on ranks ±3, FAs-X on ranks ±2, and FAs-$C_{1,2}$ on ranks ±1 (least pronounced response). After visitation, rank ±4 was most frequently 'occupied' by FAs-B_1 and slightly less frequently by FAs-Y. Highest number of ranked responses for third ranks (±3) was observed at FAs-$C_{1,2}$, and all FAs – except FAs-Y – were equally often encountered on rank ±2. Least pronounced responses (±1) were most frequently found at FAs-X. Examination of ranked responses for individual comportment parameters to some extent revealed response 'preferences' for each group of FAs that did not seem related to regime differences.

5.3.4.4.2 Regime Differences as Detected by Quantitative Comparisons

Regime differences were examined with respect to changes in prevalence of behaviour and posture parameters between periods by using two key-values: The ***difference in (period) medians*** (DiM) measured the increases/ decreases between periods observed across all sessions from FAs subjected to a given regime, while the ***median of (between-period) differences*** (MoD) constituted a measurement of **response magnitude** observed in individual sessions. Whereas rankings during visual appraisal examined consistency of response among penguins subjected to a given regime (How many?), quantitative comparisons offered the possibility of ranking regimes in accordance with differences in DiM- and MoD-values assessing the magnitude of responses (How much?).

From **pre- to during-**visitation, regime-mediated rank orders in both key-values were observed as regards the parameters 'rest' (decrease) and 'vigilance' (increase). While conduct-mediated response gradients in DiM-values were additionally found for the parameters 'breed' (increase) and 'posture – prone' (decrease), MoD-gradients detected a conduct-mediated response for the parameter 'posture – prone' (decrease), but not with respect to breeding behaviour.

From **during- to post-**visitation, rank orders for neither key-value tallied with hypothesised severity of regime or conduct for any of the parameters examined.

Comparing the periods of **pre- and post-**visitation, DiM- as well as MoD-gradients for decreased resting behaviour corresponded to hypothesised differences in severity of regimes. With respect to increased breeding behaviour, gradients in both key-values appeared conduct-mediated. Regime-mediated rank order for increased vigilance was detected by MoD-, but not by DiM-gradients.

Looking at **summed up rank positions** for both key values, gradients reliably distinguished between most and least severe regimes (FAs-Y, 3 P, L&F vs. FAs-$C_{1,2}$, 1 P, S&S), which always retained highest sums of most pronounced ranks (±4), and depicted highest sums for least pronounced ranks (±1) with a single exception (MoD from during- to post-visitation). Neither key value exhibited sensitivity with respect to the middle ranks (±2, ±3).

Given the **statistic property of median values** (i.e., relative robustness towards deviations), these results stressed that the regimes hypothesised to represent the most and least severe in terms of impact elicited a substantial unity with respect to intensity of behavioural changes across comportment parameters.

5.3.4.4.3 Regime Differences as Detected by Changes in Distribution of Phases and States

The last question of interest concerned the **structure of responses** to regimes hypothesised to differ in severity of impact (In what way do the penguins respond?).

Regime differences in ***total phase number*** (TPN) and ***time*** (TPT) were examined for selected categories, viz., 'rest', 'vigilance', 'interruptions s.l.', 'heart rate – within' (mean resting heart rate ± 2 SD), and 'heart rate – above' (do.).

Ranking FAs with respect to magnitudes of decreases/ increases (in TPN and TPT) between periods revealed several patterns that appeared animal-dependent rather than disturbance-dependent as well as rank orders that tallied with graded differences in impact of visiting regime. Animal-dependent patterns were more often found with respect to TPN, while graded differences in impact of visiting regime were more readily discernible for changes in **TPT** so that the latter must be considered **superior in terms of gauging impact of human visitation**.

From **pre- to during-**visitation, rank orders exhibited graded differences in hypothesised impact of visiting regime for the categories 'rest', 'vigilance' and 'heart rate – within'. They were not apparent in changes observed from **during- to post-**visitation, but remained notable for the categories 'rest' and 'vigilance' (the latter with the exception of one regime) upon comparison of **pre- and post-**visit proportions. Furthermore, with respect to heart rate categories, differential responses to visitor conduct (loud and fast vs. silent and slow) seemed likely.

Summing up **magnitudes of response across categories** for each regime, differences in overall *propensity to respond* (pre- to during-visitation) might have been influenced by visitor conduct with respect to FAs-B_1 and FAs-Y in terms of TPN (total phase number more affected by 'loud and fast' than by 'silent and slow' visitation). They were regime-dependent in terms of TPT. Additionally, differences in overall *propensity to continue to respond* (pre- vs. post-visitation) tallied with graded differences in impact of visiting regime for TPN, but seemed to be primarily linked to visitor conduct in terms of TPT, with the additional distinction between visitor number (less response to one visitor than to three visitors) apparent in the loud and fast regimes only. These findings might suggest **'selective decoupling'** upon waning of disturbance stimuli, with a superior impact for visitor conduct than visitor number.

5.3.4.4.4 Regime Differences – Conclusions

To put the whole matter in an eggshell, the **regime differences** hypothesised were **detectable on all levels** (How many?, How much?, In what way?) of focal-animal comportment examined, but discriminatory capacity varied between the levels.

On all levels, the greatest consistency in most pronounced responses was observed for FAs subjected to the regime hypothesised to exert the greatest impact, viz., FAs-Y (3 P, L&F), while least pronounced responses were most frequently found for FAs visited in the least severe manner, viz., FAs-C (1 P, S&S), whereas the entire gradation order was not consistently detectable.

Animal-dependent rather than regime-mediated response 'preferences' (comportment parameter), response intensities (qualitative: more/ less; quantitative: magnitude of response), and response propensities (readiness to respond/ cease responding), are suggested to merit further investigation. These need to be incorporated in future models of response, if overall results are proposed to adequately reflect focal-animal 'reality'.

6 Discussion

In order that the discussion do not turn out to constitute "an environmental effect on [the reader] which overtaxes [their] control systems"[1] (following Broom & Johnson 2000, p. 178), the outline of each results part is briefly repeated. After reflections on methods, results are discussed in the order of and according to the **seven aims** (I to VII) the study had been working towards (chapter 2.4; chapter 6.2, tab. 6-1a).

The **results** 'super-**chapter'** comprised **three parts** employing different types of evaluation:

The **first part** presented results on **focal groups**. Penguin behaviour s.l. (comprising behaviour s.s. and posture) was broadly categorised into three aspects, viz., behaviour states (behaviours lasting for longer stretches of time), behaviour events (short, abrupt behaviours) and postures. Predominant categories within each aspect were identified. Subsequently, between-period differences for entire groups (differences before, during, and after visitation), row differences within each period (differences between nests located in rows 1 to 4), and responses to different visiting regimes were examined. Responses to human visitation were compared to responses towards conspecifics.

The **second part** constituted a brief summary[2] of results on selected behaviour elements (vigilance, agonistics) and heart rate. Responses of individual **focal animals** had been correlated with human and conspecific disturbance, and magnitude and consistency of correlations were compared among disturbance types.

The **third part** considered **focal-animal** behaviour, posture, and heart rate (jointly referred to as 'comportment') from a 'topographical' point of view – the term **topography** signifying that changes in the entire 'landscape' of comportment were of interest.

This part was subdivided into **three sections** focusing on different levels of penguin comportment and asking different key questions:

- The **first section** (key question: 'How many birds do respond?') presented results obtained by qualitative visual appraisal followed by a quantitative investigation as regards **consistency** of response across focal animals and sessions: Focal-animal comportment was comprehensively visualised and subsequently appraised by examining increases/ decreases of behaviour, posture changes, and heart rate during (per visiting stage) and after (in five 2 min-intervals) human visitation. Responses to different regimes were investigated. This was complemented by an assessment of comportment during conspecific and – to a lesser degree – predator and aircraft disturbance. Results provided information as regards the number of sessions during which a given response was observed at a given visiting stage/ post-visit interval.
- The **second section** (key question: 'How much do the penguins respond?') comprised results on quantitative comparisons of behaviour and heart rate changes found during and after visitation. Responses of all focal animals together, of focal animals pooled by visiting regime, and responses observed during individual sessions were presented. Additionally, heart rate during 'visited' sessions was compared to that obtained during 'baseline' sessions (no visitation). In this section the relevant question pertained to **magnitude** of response observed.

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[1] nor the final pebble that broke the penguin's beak

[2] of a paper located in appendix 5.2-1

- In the **third section** (key question: 'In what way do the penguins respond?'), focal-animal comportment was condensed into phases (behaviour, heart rate) and states (posture), and alterations of the **'syntax'** (overall and within-system structure) and **composition** of comportment were investigated. Responses to different regimes were investigated.

6.1 Discussion of Methods

6.1.1 Conceptual Framework and Research Approach

THIS STUDY adopted an individual-based, non-invasive approach to examine the impact of human visitation and natural disturbance (by conspecifics and, to a lesser extent, predators) on incubating Adélie penguin, *Pygoscelis adeliae*, comportment (behaviour, posture, and heart rate) within the conceptual framework of **Animal Welfare Science**. It looked to experience gained in the field of **Conservation Behaviour** to operationalise human disturbance under field conditions.

The concept pursued by Animal Welfare Science lends itself to studies focusing on **individuals** (it may also be extended to larger groups). It introduces **proximate measures** (behaviour, physiology; e.g., BROOM & KIRKDEN 2004; DAWKINS 1997, 2003, 2006; DUNCAN 2005; MENDL 2001), rather than (solely) relying on ultimate ones (lifetime reproductive success, life expectancy, inclusive fitness). Measurements of welfare themselves are independent of moral considerations (Is it good/ bad to continue?, Should we change anything – or not?), but may subsequently provide the scientific basis for making such decisions (BROOM & KIRKDEN 2004). This concept can be successfully applied to captive (laboratory, farm, and companion animals) as well as free-living animals.

Operationalisation of disturbance parameters under field conditions, however, puts additional constraints on study design which rarely play a great part in laboratory or on-farm studies. The discipline of Conservation Behaviour, in contrast, has dealt with precisely these constraints for some time already and thus appeared the most likely to turn to (e.g., BEDNEKOFF & LIMA 1998; BLUMSTEIN & FERNÁNDEZ-JURICIC 2004; LIMA & BEDNEKOFF 1999; LIMA & DILL 1990; TARLOW & BLUMSTEIN 2006/ 2007; YDENBERG & DILL 1986).

In the context of THIS STUDY, adherence to the concept of Animal Welfare Science proved an eye-opener, as it markedly enhanced the observer's perception of degree of both inter- and intra-individuality in these penguins who prominently lack easy-to-catch[3] differences in outer appearance.

It is again emphasised that in THIS STUDY the 'conceptual framework of Animal Welfare Science' is restricted to the component of **human disturbance** and does not attempt an evaluation of welfare with respect to **natural conditions**. The two are related insofar as natural conditions may often result in poor animal welfare (e.g., parasites, malnourishment, and harassment by predators); under such circumstances, it is of particular importance that humans do not 'add to the bill' and thereby shove species across a threshold of no return (conservation relevance).

6.1.1.1 Methodological Precursors

Owing to its unusual adoption of conceptual framework, THIS STUDY encountered a **relative absence of methodological precursors**. The studies most closely related to the one presented here are those of GIESE (1998, on Adélie penguins, *Pygoscelis adeliae*) and NIMON (1997, on Gentoo penguins,

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[3] for human observers

P. papua). Both studies used artificial eggs and recorded penguin behaviour on video tapes. During transcriptions, Nimon noted behaviour subdivided into eight mutually exclusive categories, while Giese evaluated four main categories (with further subdivisions) of behaviour with the help of the software package 'The Observer 3.0[4]'. The broader categories chosen for focal groups in this study are thus roughly comparable to Nimon's study, whereas focal-animal second-by-second transcriptions (resulting in ethograms) can at best be approximated to (but not equated with) Giese's evaluations. In terms of duration of egg deployment and simultaneous behaviour records, this study is more closely related to Nimon's, in which artificial eggs were left in the same nest for a number of days, whereas Giese's study was designed to subject the penguins to one set[5] of visitor approaches only.

The latter procedure, viz., investigating more penguins with fewer or no repetitions, has been adopted by most of the **studies conducted since** then (cf. table 2-7 in Chapter 2.3.2), with some of them, e.g. Ellenberg & al. (2006), leaving eggs inside the same nest for consecutive days.

Three possible reasons are suggested for this trend in study design, the first being related to legal changes which render the conduction of longer-term, individually 'disruptive' (e.g., temporary removal of penguin's own eggs) studies successively more difficult to get permission for. The second pertains to scientific reality: Externally financed studies are most likely more pressed to present results to their sponsors within a relatively short timeframe; excessively time-consuming transcriptions as the ones necessitated for focal-animal evaluations presented in this study are clearly not feasible in this context. The last reason suggested concerns the field of statistics, which does not lightly accommodate repeated treatments, and/or different frequencies per entity sampled, even though mixed-effects models might indicate a possible way out of this dilemma.

6.1.1.2 Evaluation Procedures

This study is certainly unorthodox in its **poly-purpose usage of data** obtained. While data used for focal-group (behaviour s.l.) and focal-animal (comportment) analyses differed in terms of numbers of birds included, the same sets of focal-animal data were subjected to analyses examining penguin comportment with respect to two levels of complexity (behaviour elements vs. topography of behaviour systems, approx. comparable to words vs. phrases) and on three different response levels (How many?, How much?, In what way?). As this approach was adopted, however, to compare differential and perhaps **complementary strengths of analyses performed on different levels** and to examine their degree of sensitivity towards changes effected by human visitation, usage of different datasets could not have served this purpose.

6.1.1.2.1 Efficiency of Data Processing

Due to choice of sampling and transcription procedures, the two main types of evaluation (focal groups, focal animals) were very different in terms of **efficiency of data processing** (see example), which was (rather…) quickly done for a greater number of penguins in focal groups, but substantially more time-consuming for a considerably smaller number of focal animals.

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[4] Noldus Information Technology 1993

[5] each set comprising approach to three different distances, all undertaken on the same day

Example: Primary transcriptions for **focal groups**[6] involved stopping the tape every 30 s and noting for each behaviour aspect and posture the number of penguins per rows who displayed it. Additionally, number of **conspecifics** per row was taken down. For headshake counts, the tape was left running, and counts (noting nest and row) were made upon occurrence.

30 min of tape thus resulted in 60 stops plus subsequent counts, and an entire run-through to count number of headshakes (approx. min.-max. time for a 30 min-session: 3 h to 6 h).

Primary transcriptions for **focal animals**[7] involved writing down penguin behaviour and posture for each second (and necessitated frequent rewinding of tape to achieve this). For **conspecifics**, three types of motion (none, walking, and running) as well as selected behaviours were noted separately for three distances from the focal animal. For the greater part of transcriptions, focal-animal and conspecific details could not be written down simultaneously.

30 min of tape thus resulted in 1800 s to be run through at least twice (rare exception: FA mostly asleep, and conspecifics few and far between), and substantially more often, if the FA was active and/or conspecifics were many (approx. min.-max. time for a 30 min-session: 7 h to 23 h).

6.1.1.2.2 Efficacy of Results Obtained

In terms of **efficacy of results obtained** (capacities to distinguish between different stimuli/ different intensities[8] or magnitudes[9]), however, the order was most definitely reversed: The database for focal-group evaluations (Instantaneous-Scan Sampling, One-Zero Sampling, greater number of penguins) was able to detect between-period and between-regime differences only for the vastly predominant behaviour aspects (‘rest&Co’ and ‘alert’, s.b. section 6.1.3.1), whereas that for focal-animal evaluations (Continuous Recording, All-Occurrences Sampling, fewer animals) was sensitive to between-period as well as between-regime differences for a greater number of behaviour traits as well as posture and heart rate, and additionally showed that behaviour con- and disjunctions were as indicative as or even more indicative than single behaviours (e.g., scattered behaviour).

Due to the individual-based approach, focal-animal evaluations were also able to reveal substantial **inter- as well as intra-individual variability** (section 6.2.4) and suggest that these need to be incorporated rather than discounted to optimally reflect ‘penguin reality’. The proposition to ‘treasure rather than trash’ individual variation has been made time and again (e.g., Bennett 1987, for physiology; more recently and specifically, Williams 2008, for endocrinology, Ellenberg & al. 2009, with respect to habituation potential), and these authors have stressed the utility of examining causes and consequences of biological variability for, e.g., a better scientific understanding of processes of natural selection, the evolution of complex traits, and, more generally, for heuristic purposes, i.e. the detection and subsequent investigation of “interesting biological problems and

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[6] for focal groups (only ‘visited’ sessions, 30 min duration): in 2000: 20 sessions, in 2001: 10 sessions

[7] for focal animals: in 2000 (30 min-sessions): 35 visitation, 31 ’baseline’ sessions; in 2001 (45 min-sessions): 20 visitation, 33 ’baseline’ sessions

[8] A qualitative measure: With respect to within-parameter comparisons, this term is used a) when referring to initial differential degrees of expression (e.g., among groups pre-visit), or b) to degrees of changes without specifying exact magnitudinal (q.v.) values (e.g., for different agonistic behaviours: BTA, SST, AST, P, G, C; q.v.). Concerning between-parameter comparisons, resting behaviour is awarded the lowest degree of intensity, while vigilance and particularly agonistic behaviours are considered behaviours of high intensity.

[9] A quantitative measure: This term is used when referring to measured degrees of differences observed.

questions” (Bennett 1987, p. 150). No less important, the presentation of biological variability within research reports would permit future researchers to work with this aspect of reality, rather than continue to calculate around it.

6.1.1.2.3 Measures Used to Summarise Data

> “This is the tyranny of the Golden Mean: it restricts our vision of the data and narrows our conceptual framework so that we cannot take advantage of all the analytical possibilities of biological variability.” (Bennett 1987, p. 150)

Single-Key-Values were calculated to examine whether they were able to adequately reflect general comportment within a given period (mean values per period) and between-period changes (difference in [period] medians, DiM; median of [between-period] differences, MoD), respectively. While some degree of utility[10] is undeniable, their inbuilt insensitivity to fluctuations rarely proved enlightening. In conjunction with the range of values it is based on, however, a single key value may emphasise the troughs and peaks of variability, thereby helping to get a more precise understanding of this commodity.

Performance Indicator Values (PIVs) were devised to relate naturally occurring and human-induced disturbance to focal-group behaviour s.l. and focal-animal comportment. They were either tailored to reflect disturbance in predetermined timeframes of penguin comportment (focal groups, focal-animal behaviour elements) thereby focusing on the ‘disturbees’, or to the different intensities of human disturbance (focal-animal topography), emphasising the ‘disturbers’ and examining penguin comportment within the disturbance timeframe (visiting stages).

Particularly in the former case, they were found to constitute a **useful** tool to express the sum of disturbance encountered within a given interval. Absence of methodological precursors[11] , however, led to the employment of rather **normative weightings** (chpt. 4.3.4). These **could** certainly **be improved** upon, particularly with respect to heart rate, which deserves a closer look.

Even though positive **correlations between heart rate and human disturbance** were found in the majority (8 of 12) of focal birds examined, these correlations were surprisingly low (max. r^2: 0.123, i.e., explaining 12 % of the variance) if compared to findings reported in the literature.

- Wilson, R.P. & al. (1991) found heart rate of a breeding, but not currently incubating Adélie penguin, *Pygoscelis adeliae*, to almost double (from 76 bpm to 135 bpm; no information on counting-intervals) when approached by a single human slowly walking from 50 m to 4 m (over 4 min). [+78 %]
- In another study on Adélie penguins, Giese (1998; n=25 penguins, subjected to 3 different approach distances each; no information on counting-intervals) obtained similar though slightly less pronounced results during a single-person approach to 5 m (mean pre-visit resting heart rate, RHR: 82.4 bpm, SD ±11.7 bpm; increase to 126.3 bpm ±5.8). [+54 %]
- In naïve African penguins, *Spheniscus demersus*, (DeVilliers & al. unpubl. data; n=15 penguins and sessions, resp.; 20 s counting-intervals) single-person approaches resulted in an average increase in heart rate of 41 % over pre-approach RHR (pre-mean: 117 bpm, SD ±21.0). [+41 %]
- In Humboldt penguins, *S. humboldti*, Ellenberg & al. (2006) recorded heart rate increases to 198 % RHR during a direct approach to within 2 m of the nest site (12 s counting-intervals;

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1 e.g., they render reports a lot shorter

2 i.e., none were found by this author

35 penguins, average pre-visit: 104 bpm, range: 65-142 bpm; cf. publication for numbers of penguins subjected to the different treatments). [+98 %]

- As regards Royal penguins, *Eudyptes schlegeli*, Holmes & al. (2005; n=22 penguins and sessions; 5 s counting-intervals) reported a mean increase of 23 % over RHR during visitor approach to 5 m. [+23 %]

In the face of these pronounced responses reported in the literature, a correlation between heart rate and human disturbance which maximally explains no more than 12 % of overall variance appears 'pretty meagre'. While inter-individual differences in response 'preference' (see section 6.2.4) undoubtedly contribute to this result, it seems highly likely that inadequate weighting of visitor approaches for integration into the Interval Performance Indicator Value (IPIV-H) is at least equally responsible. Most importantly, heart rate was rarely found to remain elevated over longer stretches of time, whereas IPIVs reflected the continuing level of disturbance (as envisaged by the disturber) and were thus unable to flexibly 'hang on to the roller coaster structure' exhibited by heart rate values.

6.1.1.2.4 Choice of Statistics

> "Mixed model analyses were undertaken using the PROC MIXED procedure in SAS, with a GLIMMIX macro for binary response variables." (Holmes & al. 2005, p. 342)
>
> "Where necessary, I arcsine-transformed percentage data or continuous data […] prior to testing to meet assumptions of normality." (Holmes 2007, p. 2577)
>
> "We square-root-transformed recovery time data when assumptions of normality were not met […]." (Ellenberg & al. 2006, p. 99)
>
> „General linear modelling testing several factors was used to compare initial heart rate response to the standardised disturbance." (Ellenberg & al. 2009, p. 291)

This study found extensive inter- and intra-individual variation in focal-animal comportment. Consequently, all statistical analyses were performed using **non-parametric** tests (e.g. vanHeezik & Seddon 1990). This approach must certainly be considered 'archaic', as methods for data transformation have become abundantly available (see quotes above). While this lack of statistical sophistication to some extent reflects the somewhat lesser abundance of such methods at the beginning of this study, it is acknowledged that the absence of a mathematical mind and profound understanding of statistical processes, in combination with recognition of their not necessarily biology-oriented origins (e.g., Cohen 1990) and potential pitfalls (e.g., Stelzl 1982), may have biased the author towards employment of procedures that could if needs be retraced 'pen on paper'.

Besides this personal fault, variation was considered so pronounced, that its explicit depiction (e.g., visual appraisal charts) was preferred over incorporation into a single value in most analyses. Presentation of statistical results is therefore generally accompanied by or contrasted with information on magnitudes of variation (e.g., by showing boxplots or providing range-values).

6.1.2 Equipment

Video-Tapes: Video-taping penguin behaviour permitted 'serial' evaluation of simultaneously obtained responses of several birds to the same disturbance stimulus and is thus highly recommendable. Limitations arise from battery problems (see below). The substantial amount of time needed to transcribe taped recordings is to some extent alleviated by 'observation software', but manual transcriptions might render results superior to computer-effected ones if more fine-grained analyses are intended.

Artificial Eggs: Artificial eggs were chosen to avoid attachment of external devices onto penguins, since these have been demonstrated to be potentially harmful and might induce behavioural changes (e.g., Croll & al. 1991; Wilson, R.P. & Culik 1992; Wilson, R.P. & al. 1989, 1990) – especially if measurements are to last for a longer period of time (as intended during this study, in contrast to, e.g., Giese 1998, Giese & al. 1999).

It is needless to say that a **larger amount** of artificial eggs would have been preferable in a theoretical sense (or in a climatically more favourable environment), but the risk of technological failure would have likewise been augmented. Most studies have circumvented this particular problem by limiting deployment time (e.g., Giese 1998, DeVilliers & Giese 2004). Nimon (1997) reported difficulties similar to those encountered in this study.

Even though robustness of equipment and constant control of data stream were considered absolutely necessary at the time, future studies might ideally be able to count on newer technology on the market. This would enable them to do away with direct connections (cables) and employ **self-powered** and **'freewheeling' eggs**[12] with a sufficiently large storage capacity to be deployed at the beginning of incubation, and re-collected at the beginning of hatching time. In order for infrared sensors to work under these circumstances, however, alignment and contact with the incubating penguin's brood patch would have to be guaranteed (possibly by weighting the back end of electronic circuitry of the sensor, thereby inducing the sensor itself to be redirected upwards whichever way the egg has been turned).

Preliminary studies by this author (predominantly at ASPA 128, to some extent prior to beginning of this study at ASPA 132) had shown that, generally, Adélie penguins on 'non-movable' artificial eggs did not **get up** more often than neighbours incubating their natural offspring. Once standing, however, they did spend somewhat **longer trying to turn the eggs**. As Nimon & al. (1996, same finding) pointed out, this period might have been sufficient for the artificial eggs to cool down to the extent of that part of a natural egg's surface previously not in direct contact with the brood patch, thus sending the signal of 'mission accomplished' to the incubating penguin. This problem, too, could be circumvented with the freely moving eggs tentatively envisaged above.

General Equipment: Even though the equipment used benefited from the protection of the dome-tent, some data loss was incurred through wind-induced **camera** movement or temperature-related **battery** failure: Wind speed during recordings ranged from 0 km/ h to above 50 km/ h, and due to the observer's role as 'visitor' in the majority of the recorded sessions, sudden gusts could lead to a 'temporary change of focus' of the then unattended camera. Temperatures around 0°C, which were at times seriously exacerbated by wind chill, caused batteries to sometimes die off rapidly and unexpectedly, despite extra care being taken to surround spare batteries, camera, and laptop computer with the equivalent of tea-cosies. Sudden demise was particularly aggravating with respect to **laptop** batteries as it resulted in loss of not only the currently incoming data stream, but in some instances additionally caused subsequent overwriting of existent and previously saved files the computer's memory had forgotten about. Open fires and generator-driven devices being out of the question, a portable pocket heater (itself not battery-dependent…) might increase reliability and durability of batteries in future studies.

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[12] Although cable-free artificial eggs using radio-telemetry had been on the market when this study was conducted, signal transmission had been found to be seriously affected by wind-conditions.

6.1.3 Behaviour and Posture (= Behaviour s.l.)

6.1.3.1 Discriminatory Capacity of Sampling Methods

While sampling methods employed for ***focal animals*** could be considered satisfactory (if time-consuming, see section 6.1.1.2), they turned out to be of rather limited use with respect to ***focal groups***. This is to a large extent attributable to the intention with which focal-group sampling was conducted in THIS THESIS. Comparing the groups of THIS STUDY to those found in published literature, three main types of 'groups' (in the sense of 'conglomerates of individuals') can be differentiated:

- Most of the publications on human disturbance report pooled results on **'serially' approached individuals** (e.g., CEVASCO & al. 2001; DEVILLIERS & GIESE 2004, DEVILLIERS & al. unpubl. data; ELLENBERG & al. 2006, 2009; FOWLER 1999; GIESE 1998; GIESE & DEVILLIERS 2004 GIESE & al. unpubl. data; HOLMES 2004, 2007, HOLMES & al. 2005, 2005/ 2006, 2007/ 2008).

- Alternatively, **group responses** to the same stimulus have been video-taped and subsequently evaluated '**serially**' for a number of individuals (as done here with respect to focal-animal evaluations) by e.g., NIMON (1997) and GIESE & RIDDLE (1999). Focusing on individual birds, sampling categories can be as fine-grained as the investigator deems necessary, especially if the behaviour record may be replayed at leisure.

- Looking at behaviour categories used by scientists examining **group responses** of commuting penguins **'in parallel'** (e.g., BURGER & GOCHFELD 2007; WILSON, R.P. & al. 1991), disturbance parameters sampled included changes in movement (e.g., stop/ pause, stand up, move away, toboggan away), and deviations from the penguin path usually taken. With respect to within-colony disturbances and towards-colony approaches investigated by HOCKEY & HALLINAN (1981), behaviour categories were sampled at 2 min-intervals and comprised standing at the nest/ away from the nest, incubating, lying down, preening and agitated behaviour (alternate stare). Last, but not least, VANHEEZIK & SEDDON (1990) recognised seven behavioural categories when studying beach groups of penguins (prone resting, upright resting, preening, walking, bathing, and agitated/ alert behaviour – again, alternate stare). During disturbances experiments, these were sampled at 30 s-intervals.

The last study compares best to focal-group sampling of THIS THESIS, both in range of behaviours s.l. sampled and as regards sampling intervals.

Concerning the **objective behind focal-group sampling** as employed in THIS STUDY, examination of entire groups of penguins had been considered the closest approximation to the impression visitors would get when looking at a penguin colony. Focal-group Instantaneous-Scan Sampling (ISS) thus appeared a good procedure to be employed, even by 'penguinistically untrained' observers, as it did not require continuous concentration on all behaviours at once, but demanded only 'point-attentiveness' (ISS) with respect to a few rather broadly chosen categories (e.g., manipulation comprising egg- as well as nest-manipulation). The only exception had been made with respect to headshakes, a behaviour event which is not only easy to recognise, but also extremely conspicuous and can thus even be perceived if a penguin is not focused upon (All-Occurences or One-zero Sampling, OZS).

As it turned out, however, focal-group ISS was only able to capture the **'most robust' of responses**, viz., changes in the categories 'alert' (vigilance) and 'rest&Co' (resting, sleeping, yawning, 'non-committal' movements). VANHEEZIK & SEDDON (1990) likewise commented that the ratio of agitated (agitated/ alert, moving away, in the water) vs. non-agitated (prone, upright resting, preening) yielded significant differences, which might suggest that changes in at least some of their categories were not prominent enough by themselves.

In focal-group analyses performed in THIS STUDY, the behaviour states not frequently encountered (‘agonistic’, ‘flippers up’, ‘preen’, and ‘manipulate’) seemed to exhibit little overall change. Summing up the **sampling scenario** for behaviour states and posture (ISS), larger numbers of birds were scanned at 30 s-intervals and current behaviour and posture were noted for each bird. Consequently, this procedure was only able to detect alterations in behaviours, if these were displayed a) by a large proportion of the birds, and b) with sufficient predominance (frequency and/or duration) in each/ most of the birds under surveillance. As neither of these prerequisites were found with respect to the states ‘agonistic’ (few birds; frequent occurrence, but rather short bouts, which are prone to being lost in ISS; also see section 6.2.1), ‘flippers-up’ (few birds; bouts of short or medium duration, but infrequent occurrence), ‘preen’ (few birds; longer bouts, but comparatively rare occurrence), and ‘manipulate’ (more birds; frequent occurrence, but mostly short bouts), the sampling method, rather than the behaviours themselves ought to be considered insensitive at this point. As regards the ‘posture up’ (also ISS), insensitivity of sampling method to brief changes from prone to upright posture (as, e.g., seen during some displays of agonistics) is thought to have been sufficiently set off by number of birds responding and frequent occurrence of longer stretches of time for this parameter to only have effected ‘mediocre’ discrimination, instead of entirely failing to do so. Better results might be obtained if this category were sampled in a ‘one-zero’ fashion (but see below for general utility after start of hatching).

Concerning the behaviour event ‘occurrence of headshakes_yes’, the brevity of this parameter was to some extent alleviated by OZS, which, as already mentioned, was feasible while simultaneously and unfocusedly watching up to 46 birds (in this case, during video evaluations). Employing OZS with respect to the other behaviours insufficiently captured by ISS (‘agonistic’, ‘flippers up’, ‘preen’, and ‘manipulate’), however, is suggested to render focal group evaluations highly impractical (i.e., difficult on video, and next to impossible in an on-site scenario), as none of these behaviours is recognisable without concentrating on the individual (although flipper-waving also catches the unfocused eye).

In conclusion, focal-group ISS was thus (only) able to detect distinct changes occurring in predominant behaviours (shown most frequently and by the majority of individuals, i.e., ‘alert’ and ‘rest&Co’), but left a lot to be desired in terms of sensitivity to changes in less frequent behaviours and in behaviours shown by a lesser number of penguins. **It is strongly recommended that untrained observers be made aware of these limitations**.

6.1.3.2 Discriminatory Capacity of Behaviour Parameters

The category ‘posture_up’ was found to be ‘motivationally’ **confounded** once the chicks started to hatch (beginning of December), both during and outside human visitation. Human visitation might well induce penguins to bodily protect their chicks (i.e., ‘lie low’), whereas those still on eggs might be more inclined to ‘give in to nervousness’ (i.e. get up; upon adoption of a sitting posture, eggs are easier to cover than all but the smallest chicks). Averaged group records would thus be ambiguous. More importantly, there are chick-induced reasons outside human visitation for the birds to be prone (brooding or warming chicks in cold or windy weather) and to be up (feeding chicks, allowing them to cool off in ‘warm’ weather) which cannot easily be rendered into a clear baseline representing the entire focal group.

It is suggested that future studies abandon this category around hatching time, at least until the majority of chicks have hatched.

Concerning ***focal animals***, the same caveat would apply – save for the fact that it was more or less irrelevant with respect to THIS STUDY (beginning of December records all discarded, as continuous visibility of the respective FAs was severely compromised, and second-to-second transcriptions of their behaviour were thus rendered impossible). A more fine-grained distinction between different posture categories (prone, half-prone, sitting, standing) might have been preferable, but these turned out to be insufficiently distinguishable during evaluations (e.g., due to different heights of nest walls), and the idea was consequently dismissed.

As regards ***focal-animal topography***, the extremely short time (3 s) defined as constituting the shortest of behaviour **phases** may at first surprise but appears well defendable, considering the high degree of temporal variability in behaviour systems expressed. It is acknowledged, however, that resting phases of that brief a duration cannot really be considered 'very restive'.

6.1.4 Heart Rate

Manually counting heart rate records as depicted in Excel graphs was very time-consuming[13], but resulted in an intimate acquaintance with data obtained and minimised the risk of counting through artificially generated signal sequences producing heart-rate-like patterns. **20 s counting intervals** minimised extrapolation bias as well as magnitude of counting error with respect to beats-per-minute (bpm)-values employed in chapter 5.2. Using **20 s-counts** rather than extrapolated bpm-values (chpt. 5.3) eliminated extrapolation bias and helped distinguish 'suavely undulating' heart rate (±2 beats difference between counts, rather than ±6 beats between bmp-values) from disturbance-related spikes.

The procedure of **determining** mean **resting heart rate** and a tolerance band (RHR ±2 SD) has been first proposed by NEEBE & HÜPPOP (1994) and been successfully used on penguins by ELLENBERG & al. (2006, 2009). Subsequent categorisation of heart rate values as 'below', 'within', and 'above' RHR ±2SD, and treatment of stretches of heart rate in a given category as phases is considered but an extension of their concept. Examining **variation in heart rate** with the help of descriptive statistical parameters, in contrast, has not been encountered in existent literature. Given the results obtained, it would nevertheless appear to constitute a viable method of gauging changes.

6.1.5 Human Disturbance – Visiting Regimes

Human disturbance regimes had been designed according to hypothesised differences in severity, with loud and fast (L&F) visitation considered of greater impact than silent and slow (S&S) visitation, and 3 visitors (3 P) assumed to exert a greater influence than a single person (1 P). While the beginning and end of the ranking order could thus be firmly established (most severe: 3 P, L&F; least severe: 1 P, S&S), no predictions had been put forward with respect to the middle ranks.

The **switch in visiting regime** undertaken at groups B and C coincided with the beginning of hatching in some nests, which turned out to constitute a potential confounding factor, even though the majority of 'study penguins' still remained incubating: The changes wrought by greater numbers of birds returning daily (to feed chicks) as well as the generally greater impression of 'unrest' among the breeding birds (chicks are moving more than eggs, in turn inducing their parents to do the same), may have caused the lack of specific response to different regimes after the switch. For further studies, it is thus imperative to **'decouple' changes** in experimental setting from those naturally occurring in the colony examined.

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[13] Manual counts of 20 s-intervals of heart rate amounted to 5,130 graphs for 57 sessions à 30 min, and 4,185 graphs for 31 sessions à 45 min.

Differentiation between 1 visitor and 3 visitors was less pronounced than expected. This is thought to result from the **compactness of the visiting trio** (two puppets fastened to the mobile visitor) which may well have caused the loud and fast visitation events to be 'less fast' than those of a single, unencumbered visitor, while at the same time creating more movement during the silent and slow visitation event as the puppets' clothes responded to gusts of wind. More pronounced differences have been obtained in studies using 'real' groups of visitors (e.g., Burger & Gochfeld 2007, Nimon 1997: fluctuating numbers of tourists; Holmes 2004: 1 person vs. 5 people: Giese & al. unpubl. data: 3 people).

6.1.6 Non-Human Disturbance – Relevance for Response to Human Visitation

6.1.6.1 Adequacy of Indicators

The disturbance measure ***'conspecific presence'*** ('Ctotpres', obtained by Instantaneous-Scan Sampling during focal-group transcriptions) proved methodologically **inadequate** as regards the behaviour event category 'occurrence of headshakes_yes' (obtained by All-Occurrences Sampling, later transcribed as One-Zero Sampling), since it just indicated the level of conspecific presence at the sampling point but did not reflect the situation during the entire sampling interval. For further studies, it seems preferable to devise a measure that captures simultaneousness of conspecific presence/ appearance and headshake response, thus creating a form of **temporal alignment**.

Additionally, the element of 'penguin personal involvement' ought to be integrated into the disturbance measure 'conspecific presence' to check whether four nests away/ three rows back from any conspecifics, birds are considerably less inclined to react to them than in the immediate vicinity. This would necessitate including a form of **spatial alignment**.

As this study showed, the disturbance measure 'conspecific presence' can be used as a crude approximation with respect to behaviours the performance of which affects neighbouring birds (i.e., 'alert', to a lesser extent 'rest&Co'), but is shaky at best for behaviours performed in direct response to individual conspecifics (e.g., 'agonistic' behaviours).

6.1.6.2 Relevance of Conspecifics

Disturbance by conspecifics (focal animals) comprised the **presence and activities** of birds of the same species, currently not engaged in incubation. This excluded any single-bird activities on the neighbouring nests (e.g., nest stone searching in the vicinity of the focal nest) but included change-overs (nest relieves) or other marital activities for which the partner of the incubating penguin would be present.

Conspecific **presence** (focal groups) is not a good indicator for conspecific **disturbance**, as mere presence did not necessarily disturb, and usually disturbance was pretty much restricted to 'pestered' nest owners. General as it is, it is nevertheless useful for comparison with human visitation, as human presence clearly affected a wider range of nests.

Difficulties in comprehensively including conspecifics into the analyses (especially of focal-group behaviour) were mainly caused by the fact that conspecific behaviour during human visitation varied according to position and 'movement' of conspecifics before visitation:

Depending on their location, **'stationary' conspecifics** were pressed into the colony or opted to leave as the visit commenced. Conspecifics **moving along** the colony edge chose to either enter the colony or departed more quickly (left the colony). **Approaching** conspecifics would at times delay passing the visited part until the visitor left, thus causing considerable movement after the visitor's departure.

A **further complication** resulted from THIS OBSERVER's inability to reliably identify **nesting partners** (as opposed to 'loafers'/ non-partners), unless a direct change-over or its immediate aftermath had been recorded. A given penguin's partner increased the incubating bird's propensity to stand up (mutual display, change-over, egg/ nest rearrangement by newly arrived penguin), while an incubating penguin's response to penguins other than their mate was dependent on the behaviour of the 'strangers': At times the incubating bird would sit more tightly (protection of eggs and/or territory), while the 'same' situation elicited an upright posture and agonistic responses (defensive or offensive) in other cases/ penguins. Since there were only very few times when a conspecific could unmistakeably/ reliably be identified as the partner of a focal animal (e.g. after an observed change-over), these instances were not counted separately, i.e. movement of the respective individual added to the general conspecific disturbance like that of any 'stranger'. To check for differences, the alternative (excluding the partner when known) was also examined for selected FAs (B4-2, 23.11.2000; A5-2, 28.11.2000) but did not yield substantially different results. In further studies, however, partners to incubating focal birds should ideally be evaluated separately.

To render matters even more complex, MORENO & al. (1995a, b) as well as VIÑUELA & al. (1995) found **individual and sex-based differences** in Chinstrap penguin (*P. antarctica*) nest theft behaviour. Should a similar variability exist in Adélie penguins, past experiences might single out 'specific conspecifics' to certain (?) focal animals.

Conspecifics are proposed to constitute an important **background** source of potential disturbance to penguins incubating in colonies composed of small territories. Their effect should be included in analyses of the incubating birds' responsiveness to human visitation – if only to be eliminated when visitation impact is focused upon. Focal-group analyses proved too 'coarse' to identify beyond doubt the reciprocal interactions between conspecific and human impacts. They did, however, make a reasonably good case for pre-visit variability of conspecific presence to exert an influence on during-visit responsiveness of focal penguins.

In conclusion, knowledge of the general level of conspecific presence/ activity is suggested to be an important source of information as it provides an – albeit limited – insight into differences in 'background noise' between study groups.

6.1.6.3 Relevance of Predators

The experimental approach followed in THIS STUDY was strictly limited to controlled visiting experiments by humans, but did not include manipulation of conspecifics or manipulation of predators (for the latter, e.g., by placing baits, e.g., GIESE 1998). Observations on **predator presence and activity** were **collected empirically** (ad-lib. sampling) and could thus not be analysed quantitatively. On a qualitative basis, sampling points/ intervals were excluded from analyses of human impact if behaviour of the majority of the focal group could clearly be attributed to predator presence or activity. While this did not allow statistically confirmed conclusions on impact of predators during visitation, the procedure helped to eliminate responses obviously motivated by predators. Predator presence/ activity did not seem to vary among the groups included[14] in focal-group analyses.

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[14] Situated on a hilltop, group A (not included in FG-evaluations) 'received' more overflights than the other groups.

Qualitative observations suggest that direct predator attacks on a nest within the focal group as well as low overflights momentarily drew the group's attention away from any type of visitation and could thus be considered to exert a stronger 'point-impact[15]' than humans at that moment.

As outlined for conspecific presence, human visitation under these circumstances ought to be viewed as an additional, rather than an alternative source of disturbance. In contrast to conspecifics, however, human visitation is considered to represent the continuous background to which predator threat is added.

6.1.6.4 Relevance of Aircraft Noise

In THIS STUDY, aircraft noise was encountered too rarely to permit any conclusions. As other studies have shown (e.g., CULIK & al. 1990a; HARRIS 2005; WILSON, R.P. & al. 1991), aircraft noise and particularly aircraft presence has a generally devastating effect on penguin comportment as well as breeding success (e.g., CULIK & WILSON, R.P. 1991; also see overview provided in chpt. 2).

6.1.7 Climatic Conditions – Relevance for Response to Human Visitation

6.1.7.1 Considerations Pertaining to THIS STUDY

As different comportment under different climatic conditions did seem highly likely (e.g., CULIK & al. 1989), care was taken to include a period of time immediately prior to each visit and to thereby create a daily 'baseline' to refer to when examining changes during visitation (using the animals as their own control, e.g., BALDOCK & SIBLY 1990). Climate-related data were collected with respect to temperature, wind conditions, precipitation, and cloud cover. Upon opportunity (and mainly reported in footnotes), same-day behaviour of different penguins was compared. While individual penguins were observed to behave differently on different days (and under different weather conditions), there was no general trend for unanimously favoured behaviour systems during cold, 'warm' (around 0°C), snowy, or windy weather observable.

6.1.7.2 Considerations Pertaining to Long-Term Trends

As already mentioned, natural conditions often lean towards poor animal welfare (q.v.); and long-term changes in specific factors (e.g., climate) may either exacerbate or alleviate the overall challenge the penguins have to cope with.

The **potential climatic impact of global change** did not form part of THIS STUDY. It should therefore be emphasised that even if Adélie penguins experienced a net gain in terms of climatic conditions changing in their favour, this would not alter the relevance of findings as regards the impact of human disturbance, but said net gain might improve the birds' ability to cope with human visitation. As it is, Adélie penguins in the area of the Antarctic Peninsula and its adjacent islands appear to have become more vulnerable to additional challenges, since their numbers are waning in line with a reported rise in temperatures. CARLINI & al. 2005 (p. 156) state that "[e]arly census data showed that chinstraps expanded their range southward along the western side of the Antarctic Peninsula, into areas historically dominated by Adélie penguins (PONCET & PONCET 1987)." They go on to suggest that "[c]urrent trends in climatic change with its effect on ice distribution and krill availability seem to create more favourite conditions for chinstrap penguins than for Adélie penguins in areas where these species co-occur (LYNNES & al. 2002)" (see, e.g., TRIVELPIECE & VOLKMAN 1979

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[15] cf. stiletto heel vs. elephant foot

for further reflections on nest-site competition between Adélies and Chinstraps). In ASPA 132 (STUDY SITE), in contrast, Chinstrap penguins were few to begin with and have apparently ceased to frequent the area for breeding purposes (M. GASCO, pers. comm. 2010); here, numbers of Gentoo penguins (*P. papua*) are increasing and these seem to replace Adélie penguins to some extent (in less steeply inclined areas). Alterations like these are unlikely to affect Adélie penguins at all breeding locations alike, as Antarctica does not respond homogenously to climatic change.

6.2 Discussion of Results

Results presented in the three parts (focal groups; focal animal behaviour elements and heart rate; focal animal topography) contributed differently to the aims outlined for THIS THESIS. Table 6-1a, b gives an overview with respect to aims formulated (I to VII, tab. 6-1-a) and types of results obtained (1 to 32, tab. 6-1-b), with numbers of results relevant to each aim listed beneath formulation of the aim itself. As mentioned above, results are discussed in the order of and according to these aims. For each aim, the null hypothesis, proposed working hypothesis/ hypotheses, and – if applicable – specific assumptions (e.g., with respect to ranking order of severity of visiting regimes) are repeated. As regards the first two aims (between-period differences in behaviour s.l., between-period differences in heart rate) order of discussion additionally follows order of results presented (see beginning of chapter for summary).

Table 6-1: Overview of a) Study Aims Formulated (I to VII) and b) Results Presented (1 to 32). Aims classified as either scientific or applicable; results classified according to focus (groups, animals) and structural complexity (elements, topography). Results contributing to a given aim are listed underneath formulation of aim itself. Different results parts distinguished by enumeration of section (focal groups, focal-animal ‘elementary’ evaluations) or section and subsection (focal-animal topography). ‘Bonus tracks’ comprise additional findings not directly related to any aim. Elem.: elements; Quant. Comp.: quantitative comparisons.

Table 6-1a: Overview of Study Aims Formulated (I to VII) .

Aims	No.	Overview of Aims of Study
Scientific	I	**Examine the Impact of Human Visitation on Incubating Penguins' Behaviour/ Posture**
		1, 2, 7, 9, 17, 22-24, 26-28
	II	**Examine the Impact of Human Visitation on Incubating Penguins' Heart Rate**
		7, 10, 19-21, 29-31
	III	**Examine the Extent of Individuality (Coping Strategies) re Response to Human Visitation**
		7, 13-15
	IV	**Compare the Impact of Human Visitation to that of Conspecific Disturbance**
		3, 4, 6, 7, 11
	V	**Examine the Impact of Different Visiting Regimes (Visitor Conduct and Number)**
		5, 16, 18, 25, 32
Applicable	VI	**Find Indicative Behaviours/ Postures**
		1, 7, 9, 13-15, 17, 22-24, 26-28
	VII	**Find Threshold Distances**
		9, 13-15
'Bonus Tracks'		**Additional Information on Non-Human Disturbance**
		8, 12

Table 6-1b: Overview of Results Presented (1 to 32).

		Results-Chapter	No.	Overview of Results Presented for Focal Groups
States, Event, Posture		5.1	1	Behaviour s.l. before, during, and after Human Visitation
		5.1	2	Row Differences before, during, and after Human Visitation
		5.1	3	Relationship between Intensity of Responses and 'Type of Disturbance' – Conspecifics outside Human Visitation
		5.1	4	Relationship between Intensity of Responses and 'Type of Disturbance' – Conspecifics during Human Visitation
		5.1	5	Relationship between Intensity of Responses and 'Type of Disturbance' – Human Visitation
		5.1	6	Comparison of Responses to Conspecific Presence during Human Visitation with Those Elicited by Human Visitation
				Overview of Results Presented for Focal Animals
Elem.		5.2	7	Vigilance, Agonistics, and Heart Rate (bpm) during Human and Conspecific Disturbance
Topography	**Visual Appraisal**	5.3.1	8	Impact of Conspecific Movement before Human Visitation on Behaviour, Posture, and Heart Rate during and after Visitation
		5.3.1	9	Behavioural and Postural Topography before, during (per Visiting Stage), and after Human Visitation
		5.3.1	10	Heart Rate Topography before, during (per Visiting Stage), and after Human Visitation
		5.3.1	11	Behavioural, Postural, and Heart Rate Topography during Conspecific Presence and Action
		5.3.1	12	Behavioural, Postural, and Heart Rate Topography during Predator Presence/ Attacks and during Aircraft Noise
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		5.3.3	31	Category Phase Number and Category Phase Time for Each Heart Rate Category (*indCats-indScls*)
		5.3.3	32	Regime Differences in Heart Rate (Within, Above) - Total Phase Number and Time (*indCats-allScls*)

Preceding this aim-wise discussion, **'miscellaneous' findings** which appear to be of interest but are not directly related to a specific aim are briefly considered.

With respect to literature references, comparison of results obtained in THIS STUDY with those found in published reports is easily effected in terms of **direction** of changes observed. In terms of **magnitude**[16] and **intensity**[17] of behavioural, postural, and heart rate changes, however, differences in biology of penguin species (e.g., degree of likeliness to show agonistic behaviours; burrow- vs. bowl-nesting vs. egg-on-feet incubation), and study (e.g., number of penguins, time of breeding cycle) as well as experimental designs (number of approaches to each penguin; number/ conduct of people, duration of visit, stages/ distances tested during visitation; durations of pre- and post-visit periods), generally complicate direct comparison with these studies. Furthermore, no previous studies on **structural**[18] **alterations** in comportment ('syntax') were encountered.

EGGLETON & SIEGFRIED (1979, p. 166) have aptly described this as

> "[…] the obvious problem of 'comparability' caused by different observers, with varying ethological expertise during the last 30 years or so recording different descriptions and using different names for displays of the same and different species whose different populations were studied under different conditions at different places."

This being said, examples of ranges in magnitude/ intensity are provided whenever they could be rendered comparable; detailed excerpts of all the disturbance studies reviewed are presented in appendix 2-2. Figures taken from the literature are given 'as reported'. Figures from THIS STUDY are rounded off as regards proportions $\geq$ ±1 %, i.e., exact proportions are provided for values < ±1 % only.

6.2.1 Miscellaneous

6.2.1.1 Impact of Egg-Deployment

To gauge **impact of egg-deployment** on subsequent behaviour and heart rate responses, birds resident on the nest during placement of the artificial egg had been paint-marked and could thus be distinguished from their naïve partners.

Preliminary analyses revealed substantial day-to-day variation within as well as between heart rate of individuals, but no consistent differences between birds that had been present during placement of the artificial egg and their respective partners. This result tallies with findings on Gentoo penguins (*Pygoscelis papua*) presented in NIMON (1997): She likewise did not detect differences in response to humans between the penguins present during placement of the artificial egg and their naïve partners. Her conclusion (ibid., p. 162) that "one controlled 2.5 minute period of close approach to the nest, without capture or handling of the penguin, did not bias [the non-

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[16] Magnitude of changes in comportment: That which is conceived of as measurable (WEBSTER 2003). A quantitative measure: This term is used when referring to directly measured degrees of differences observed.

[17] Intensity of comportment: Relative strength or degree of a quality or force (WEBSTER 2003). A qualitative measure: With respect to within-parameter comparisons, this term is used when referring to initial differential degrees of expression (e.g., among groups pre-visit), or to degrees of changes without specifying exact magnitudinal (q.v.) values (e.g., for different agonistic behaviours: BTA, SST, AST, P, G, C; q.v.). Concerning between-parameter comparisons, resting behaviour is awarded the lowest degree of intensity, while vigilance and particularly agonistic behaviours are considered behaviours of high intensity.

[18] The structural component encompasses the duration and number of phases/ states, and can be thought of as the 'syntax' of comportment. If the 'syntax' is altered, this leads to pattern changes in overall topography of comportment (for behaviour, e.g., shorter phases irrespective of contents, i.e., behaviour system) and/or pattern changes within individual comportment parameters (e.g., shorter phases of 'rest').

naïve penguin's] subsequent response to human visitors"[19] is supported by findings from THIS STUDY.

6.2.1.2 Increased Resting Behaviour Post-Visit

Visual appraisal indicated that post-visit increases in resting behaviour (i.e., exceeding the 'baseline' of pre-visit behaviour) rose rather steeply (from 8 % to 18 %) between the first and second post-visit interval (1-2 min to 3-4 min post-visit) and subsequently 'oscillated' between 20 % and 25 % for the remainder of the recorded time, i.e., in 20 % to 25 % of all sessions appraised (n=51), resting behaviour post-visit exceeded pre-visit levels.

This result might be puzzling at first sight but is better understood by examination of individual sessions: FA B3-1 (24.11.2000), for instance, showed moderate proportions of resting behaviour prior to visitation (44 %; with all behaviours per period = 100 %), accompanied by frequent breeding activity (20 %). After visitation, resting behaviour increased (88 %), 'to the detriment' of breeding behaviour (2 %). These proportions capture overall time spent in a particular system during the entire period; if they are combined with distribution of behaviours as depicted by the topography charts (appendix 5.3.1-1), it becomes evident that B3-1 'settled into' predominant resting in the second post-visit interval (with some breeding and rather more vigilance behaviour present in the first post-visit interval).

FA B3-2 (21.11.2000) may serve as another example: Resting behaviour pre-visit (61 %) was lower than post-visit (82 %), while vigilance behaviour prior to (38 %) was considerably higher than after visitation (12 %). For this focal animal, the topography chart shows that the first post-visit interval was likewise (particularly initially) characterised by little resting and considerable vigilance and breeding behaviour, which were almost completely absent in the following post-visit intervals.

These findings again emphasise the complexity of results if responses of different individuals are combined, and point to the utility of being able to follow 'each thread in the tapestry'.

6.2.1.3 Absence of Regime-Graded Responses in Agonistic Behaviour

> "The individuals comprising a community of Adélie penguins (*Pygoscelis adeliae*) may appear morphologically similar, but are behaviourally quite distinct." (SPURR 1974, p. 611)
>
> "The Adélie is the most aggressive of the Pygoscelid Penguins. Individual birds vary greatly according to temperament, sex, the different phases of the breeding season, and their state of nourishment during the fasting periods. Thus when a man meets a party of Adélies away from the breeding area, some may flee, others walk up nervously, though a few may even attack with bills and flippers with the same fury as is shown in defence of nest-sites." (SLADEN 1958, p. 37)

Using visual appraisal to examine **regime-mediated response differences**, these were found at one or more visiting stages and/or post-visit intervals for all parameters examined – except for agonistic behaviours. Thus, while the parameter exhibited clear changes during visitation, these indicated an overall graded response with respect to visitor distance (the closer, the more), but did not tally with hypothesised differences in severity of impact of different visiting regimes.

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[19] and thus did not necessitate establishment of two different treatment groups

Some previous studies likewise found agonistic behaviours to increase during human visitation (e.g., Giese 1998, for Adélie penguins; Holmes 2007, Holmes & al. 2007/ 2008, for Royal penguins and King penguins; Yorio & Boersma 1992, Fowler 1999, Walker & al. 2006, for Magellanic penguins, *Spheniscus magellanicus*; Ellenberg & al. 2006, for Humboldt penguins, *S. humboldti*; and DeVilliers & Giese 2004, for African penguins, *S. demersus*). Holmes & al. (2007/ 2008) but not Nimon (1997) observed threat behaviours towards/ in the presence of humans in Gentoo penguins (*Pygoscelis papua*), but little information could be obtained as regards differential responses to different visiting regimes.

The **lack of a 'communally graded agonistic response'** to changes in severity of stimulus is suggested to result from inter-individual differences in the penguins subjected to these regimes.

Penney (1968) reported the alternate stare to occur in both female and male Adélie penguins once the birds were incubating (while it was more restricted to males prior to egg-laying), whereas the agonistic display of bill-to-axilla was employed much more often – though not exclusively – by males than females. His findings might be interpreted as support for a **supposed sex bias** in terms of propensity to respond agonistically to human visitation.

Spurr (1974) examined individual differences in aggressiveness of Adélie penguins by presenting them with a penguin-dummy. Similar to Penney (1968), he found distinct sex differences prior to egg-laying, with male aggressive responses being more intense and more frequent in occurrence than female responses. Soon after the first egg was laid, however, these differences disappeared – as long as both male and female responses were averaged per sex class (average mated male vs. average mated female). Looking at each of the breeding pairs, in contrast, revealed "some marked individual differences" (Spurr 1974, p. 612): Of the 45 breeding pairs examined, 14 pairs comprised significantly more aggressive males, while in 11 pairs the females were significantly more aggressive (as measured by score of pecks per minute given to the dummy). These findings might point to **different 'temperaments'**, which complemented each other in the 25 pairs (the remaining 20 pairs did not exhibit such an 'unbalanced' degree of aggression).

As Sladen (1958, see quote above) mentioned, additional differences in propensity to show aggressive behaviour may result from **state of nourishment** and **phase of breeding cycle**. Although the latter is fairly synchronised within a given colony, the former might have contributed to the lack of a 'communally graded agonistic response', as time since last change-over would have determined the degree to which individual penguins might have suffered from the effects of prolonged fasting.

It is concluded that, while sexual differences may have contributed to the finding, a greater part of observed individuality was most probably due to differences in 'temperament' and state of nourishment. Since all of these factors influence behaviour of individual penguins regardless of the visiting regime they are subjected to, no graded responses should be expected.

6.2.2 Aim I: Impact of Human Visitation on Behaviour and Posture (= Behaviour s.l.)

H_0: There will be no differences in behaviour s.l. before, during, and after human visitation

- H_{1A}: Behaviour s.l. during visitation will differ from behaviour s.l. before visitation.
- H_{1B}: Behaviour s.l. during visitation will differ from behaviour s.l. after visitation.
- H_{1C}: Behaviour s.l. after visitation will differ from behaviour s.l. before visitation.

Recapitulation: The difference between **pre- and during-**visitation is considered to reflect the immediate effect of visitation, while the difference between **during- and post-**visitation is suggested to shed light on the focal animals' continuing/ waning response after withdrawal of the stimulus. The difference between **pre- and post-**visitation thus gives an indication as to the extent to which the animals have managed or failed to recover during the post-visit period.

6.2.2.1 Conclusions – Between-Period Differences in Behaviour s.l.

With respect to absence of between-period differences in behaviour s.l., H_0 was successfully refuted.

In conclusion, human visitation elicited substantial changes in incubating Adélie penguins' behaviour and to a lesser extent posture, both during the visit itself and after visitation. Alterations were still detectable in the fourth **row** into the colony; they were observed with respect to **consistency** (numbers of penguins responding), **magnitude** (decreases/ increases in prevalence of behaviours/ postures), the overall **composition** of behaviour/ distribution of the two postures, as well as in terms of changes in the structure of behaviour/ posture (**'syntax'**).

Changes were most easily discernible for predominant behaviours (resting: fewer penguins, less overall time, shorter phase durations, and vigilance: more penguins, more overall time, longer phase durations), but could be detected in **all parameters** examined.

While direction of response tallied well with **literature** reports, disparities with respect to magnitudes of response are suggested to derive from differences in species and experimental/ study design on the one hand, and differential perception of the stimulus presented on the other.

Following, results pertaining to the question of between-period differences in behaviour s.l. will be discussed in detail.

6.2.2.2 Placing Results Obtained into Context

6.2.2.2.1 Focal Groups: Spatial Extent of Impact of Human Visitation

To examine the extent to which the effect of human disturbance might reach into a given colony, focal-group analyses in THIS STUDY included penguins nesting in four rows of increasing distance from the colony edge. While there were no row-differences with respect to predominant behaviours expressed ('alert' and/or 'rest&Co', 'headshakes_none', and 'posture_prone'), R1-birds (first row = periphery) were frequently observed to exhibit stronger changes (i.e., greater increases for 'alert' and 'headshakes_yes'; greater decreases for 'rest&Co') during visitation than birds nesting in the following rows. Between-row differences, however, were statistically not significant (pair-wise Friedman-test).

Preceding studies – not necessarily predominantly concerned with human disturbance – had mostly contrasted **peripherally** nesting penguins with **centrally** nesting ones, using slightly different definitions of ‘central’ (e.g., Penney 1968 p. 96: “at least one other nest between it and the edge”; Nimon 1997, p. 50: “at least two nest sites from the exposed outer edge of the group”; Tenaza 1971, p. 81: “central in relation to six nearest neighbors [sic] rather than central within the colony”). Tenaza (1971) found peripherally[20] nesting Adélie penguins (*Pygoscelis adeliae*) fleeing more readily when approached by the investigator and proposed two possible explanations: Central nesters could either be ‘trapped’ by hostile neighbours, or peripheral nesters could alternatively exhibit stronger escape tendencies. The former explanation tallies with Penney’s (1968) finding of Adélie colonies never exceeding a maximum in-depth (from periphery to centre) of 12 m – this apparently being the maximum of successive hostile encounters an Adélie penguin was able to sustain. Spurr (1974, no verbal definition presented; fig. 4 ibid. suggests only outermost row of nests to constitute periphery) reported an increased likelihood of high-scoring aggression for centrally as compared to peripherally nesting Adélie penguins.

With respect to nest location[21] being influenced by age and breeding experience, Ainley states (2002, p. 187) that young Adélie penguins tend to establish their nest sites either on the periphery or “well into the interior” (four or more sites from the periphery) of a contiguous group of breeding penguins, thereby incurring either a higher risk of predation by skuas or higher degrees of aggression each time they leave or return to their nest sites[22]. Nimon (1997) found that centrally (=R3) and peripherally (R1, R2) nesting Gentoo penguins (*Pygoscelis papua*) did not respond differently[23] to approaches of single visitors or visitors in small and large groups, while a number of other studies (e.g., Holmes 2004, 2007, Holmes & al. 2005, 2005/ 2006, 2007/ 2008) exclusively selected peripheral nests, because these penguins were perceived to receive ‘the brunt of human visitation’.

As mentioned above, pair-wise Friedman-tests in this study did not detect significant differences between the rows (with the exception of two [24] cases), and results presented on focal groups were therefore based on total numbers without further consideration of row distinctions.

This result is suggested to indicate that the frequently greater responses observed for R1 birds form part of a **gradually lessening response continuum**, with reactions detectable until at least (this study did not look any further into the colony) the fourth row (and a gradient most stringently observed in groups X and Y), rather than an abrupt decline of response after the first row. Results on focal groups ($R1_{inexp.}$; $R2\&R3_{exp.}$; $R4_{inexp., exp.}$; i.e., mainly experienced breeders) need to be viewed in this light, especially when contrasting them with results on focal-animals, as deployment of artificial eggs had dictated these birds to be situated in first and second[25] rows only (mostly R1, some R2, i.e., mainly inexperienced breeders).

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[20] with the term ‘peripheral’ pertaining to penguins not surrounded by other nests and thus equal to definitions of periphery used by the other authors, with the possible exception of Nimon (1997).

[21] ‘centrally’ nesting penguins: “with at least one nest between theirs and the periphery”; tab. 5.5 ibid. suggests only outermost row of nests to constitute periphery

[22] Ainley (2002, p. 188) also points out that Tenaza’s detection of substantial differences in breeding success between peripheral and central nesters was likely due to the fact that he was thereby comparing the breeding success of a sample comprising “the highest possible proportion of young birds” (inexperienced breeders, periphery) to that of a sample of “the highest possible proportion of oldest birds” (experienced breeders, two to three nest sites into the colony).

[23] If Ainley’s (2002) observations applied to Gentoo penguins as well, both Nimon’s (1997) samples would have included experienced as well as inexperienced breeders, which might explain this lack of (mean) response differences.

[24] during-visit differences between R1 and R4 for ‘alert’ as well as ‘rest&Co’ in dataset B_1 (1 P, L&F)

[25] Given the usual spacing of nests, those of second-row birds could be approached by squeezing through in-between two first-row territories so that no bird needed to be ‘loomed over’. Violation of two boundaries at the same time at least made for a bilaterally tidy pattern of peck-bruises.

6.2.2.2.2 Focal Groups: Between-Period Differences (And Lack Thereof)

With respect to ***focal groups***, distinct **differences** from **pre- to during-**visitation were found for the behaviour states ‘alert’ (vigilance) and ‘rest&Co’ (resting, sleeping, yawning, ‘non-committal’ movements), and small differences as regards ‘occurrence of headshakes_yes’ (behaviour event) as well as ‘posture_up’. Direction of trends was reversed from **during- to after-**visitation, and there was next to no difference between **pre- and post-**visit periods.

Reasons for lack of differences concerning the remaining behaviour categories have been presented in section 6.1.3.1. Here, the **‘relative sameness’** between pre- and post-visit periods found for behaviours and posture that had clearly altered during visitation (‘alert’, ‘rest&Co’, and less markedly ‘headshakes_yes’ and ‘posture_up’) is of interest, as it does at first glance suggest a ‘relative robustness’ of the penguin groups visited. At this point, it is necessary to recall that this result (merely) states that across all sampling points per period (prior to vs. after visitation), ‘approximately the same number of penguins’ (proportionalised with the help of the Penguin-Unit Index, PUI; chpt. 5.1.1) was assigned to each of the categories examined, whereas during visitation a lower PUI had been calculated with respect to rest, and higher PUIs with respect to the other categories. The result cannot convey information on differential rising/ waning of responses (e.g., steep drop initially, tapering out towards the end), on continuation[26] , or on intensity (e.g., moderate or intense vigilance) of behaviours expressed, and what it most certainly cannot do, is trace relative differences in recovery of individuals.

6.2.2.2.3 Focal Animals – Behaviour Elements: Correlation with Human Visitation

Changes in ***focal-animal behaviour elements*** (measured as the proportion of behaviour shown per 20 s-interval) indicated that increases in vigilance were significantly correlated (max. r^2: 0.308, i.e. explaining 31 % of total variance) with increases in intensity of human disturbance (as depicted by the Interval Performance Indicator Value for Human Visitation, IPIV-H; chpt. 4). This result corroborates focal-group findings, insofar as it additionally adds the hitherto missing aspects of changes in response intensity (rising/ waning), and continuation. With respect to agonistic elements, it additionally indicates that distinct responses were found in half of the birds examined (max. r^2: 0.273).

Reasons for pronounced individuality of agonistic behaviour have been proposed in section 6.2.1. At this stage it appears important to realise that the response shown by these birds (which, after all, were part of the focal groups) could actually be considered more obvious (agonistics being a more forceful expression of disagreement with current conditions than vigilance), but went entirely undetected by focal-group analyses.

6.2.2.2.4 Focal Animals – Topography: Changes in Behaviour s.l. Detected by Visual Appraisal

The complete visualisation of focal-animal comportment (***topography charts***) was undertaken for 51 sessions of 19 FAs. Proportions depicted number of sessions in which birds responded with increases/ decreases in the respective categories (Key question: How many?). In its key question, this evaluation was thus similar to that of focal groups, and confirmation of focal-group results **during-visitation** concerning the categories ‘alert’ (vigilance), and ‘rest&Co’ (resting, sleeping, yawning, ‘non-committal’ movements) did not come unexpectedly. In addition, however, this

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[26] Degree of continuation is impossible to gauge using Instantaneous-Scan Sampling: ‘You can wave your head about for as much as you like, so long as it’s seen in the resting position on the instantaneous-scan sampling point.’/ ‘You can be as motionless as you please, if you move your head at the sampling point, you’ll be counted as vigilant.’

evaluation was able to show that none of the comportment parameters examined was unaffected by human visitation. Moreover, and in contrast to focal-group findings (‘complete recovery’), visual appraisal indicated only a **relative recovery** (trend towards, but not fully effected) within the post-visit period (10 min) for all of the comportment parameters, and suggested that at least for some birds, this time was not sufficient to recuperate and return to the comportment exhibited prior to visitation.

In terms of **direction** of changes observed, it has already been stated in chapter 2 that increased vigilance and decreased resting in response to human **visitation** have been reported by a great number of studies for Adélie penguin, *Pygoscelis adeliae* (e.g., Ainley 1974, Culik & al. 1989, 1990a, Giese 1998, and Wilson, R.P. & al. 1991), as well as for other penguin species (e.g., for Gentoo penguins, *P. papua*, Nimon 1997, Holmes 2004, 2007, and Holmes & al. 2005/ 2006, 2007/ 2008; for Royal penguins, *Eudyptes schlegeli*, Holmes 2007, and Holmes & al. 2005, 2007/ 2008; for King penguins, *Aptenodytes patagonicus*, Holmes 2007, and Holmes & al. 2007/ 2008; for Emperor penguins, *A. forsteri*, Burger & Gochfeld 2007; and for African penguins, *Spheniscus demersus*, vanHeezik & Seddon 1990, and DeVilliers & Giese 2004). The most notable **exception** appears to be the report from Ellenberg & al. (2004) who found Snares crested penguins, *Eudyptes robustus*, to barely respond to human presence.

Concerning **magnitude of responses**, most studies report mean values for increases within categories across all focal animals (How much?); these are comparable to results on quantitative comparisons of prevalence in this study (see following section). Results on inter- and intra-individual **consistency of response** (numbers/ proportions of penguins responding → How many?), in contrast, are more sparsely encountered. In Gentoo penguins (Nimon 1997), for instance, approach by a larger group of 15 or more visitors resulted in 65% of the penguins (12 samples from 8 penguins) adopting alert ‘postures’ [sic], beginning when the group had approached to a 15-20 m distance, but behavioural response showed a marked reduction (to 49%) when people had reached the 5 m distance and did not approach any closer.

Despite the far larger number of visitors, Nimon’s study birds thus did not respond as consistently with respect to vigilance behaviour, as the Adélies examined in this study (58 % during approach to 5 m, 75 % during visitor stay at 5 m, 81 % at 3 m). Additionally, Adélie penguins in this study exhibited an increase in response between visitor approach to and stay at 5 m.

Findings reported in the literature which concern the other behaviours examined in this study likewise corroborate results obtained during visual appraisal in most cases:

The ‘meta-comportment’ parameter ‘scattered behaviour’ (connoting a quick succession of switches between two or more behaviour systems) had not been applied previously. In this study, marked increases **during** visitation appeared linked to visitor stay at distances of 5 m (46 %) and 3 m (43 %), respectively, as well as to visitor retreat (36 %). **After** visitation, scattered behaviour remained at approximately the level calculated during retreat for the first and second post-visit intervals (37 %, and 38 %, resp.). Scattered behaviour seemed to indicate indecision and/or apprehension (in the face of a stimulus that does not come closer/ that might return; penguin-perspective). This assumption tallies well with the finding that decreases in scattered behaviour during visitation mainly occurred when vigilance became predominant. Rather than representing a truly ‘novel’ parameter, scattered behaviour might thus reflect the overall impression gained when displacement activities (Broom & Johnson 2000; Immelmann & Beer 1992) encroach upon normal performance.

In chapter 2, it was stated that findings on preening behaviour (comfort) appeared to differ between species, with Ainley (1974) as well as Giese (1998) reporting no changes in preening behaviour of visited Adélie penguins, *Pygoscelis adeliae*, either **during**, or **after** visitation. Ainley (1974) did, however, observe an increase in both-wings-stretches and an increase in rapid-wing-flaps **during** human presence. In contrast, preening behaviour of African penguins, *Spheniscus demersus* (Hockey & Hallinan 1981, adults and chicks), had been observed to completely cease[27] at 20 m **during** human approach from 60 m to 10 m (initial proportions: adults 20 % of 184; chicks: 56 % of 24). That of Gentoo penguins, *P. papua* (classified as self-maintenance), was found to increase, particularly 5-10 min **post-visit** (Holmes & al. 2005 for egg stage[28], 2007/ 2008 for guard stage[29]).

In this study, longer stretches of comfort behaviour (preening) or repeated occurrences of shorter bouts (e.g., yawning, stretching) were rarely observed to begin with (14 of 51 sessions). Within this 'unrepresentative sample', the three instances of extensive preening behaviour pre-visit were invariably found to lead to considerable decline **during** and subsequent cessation **after** visitation. After visitation, the greatest alteration in comfort behaviour with respect to both increases and decreases was found in the third post-visit interval (5-6 min: increase in 6 and decrease in 4 of 13 sessions). While results on preening **during** visitation thus lean towards those on African penguins in terms of direction and magnitude of change (Hockey & Hallinan 1981), a 'temporal' similarity in changes in comfort behaviour **after** visitation is seen with results on Gentoo penguins reported by Holmes & al. (2005, 2007/ 2008).

Changes in breeding behaviour **during** human visitation (including standing up, shifting on nest, and nest abandonment, with the latter not observed as a direct cause of visitation in this study) were found for Adélie penguins, *Pygoscelis adeliae* (Giese 1998, see below at posture), as well as other penguin species (e.g., Magellanic penguins, *Spheniscus magellanicus*, Fowler 1999; African penguins, *S. demersus*, Hockey & Hallinan 1981, DeVilliers & Giese 2004). **After** but not during visitation, it was found to increase in Gentoo penguin, *P. papua*, particularly 5-10 min **post-visit** (Holmes 2007, Holmes & al. 2005/ 2006, 2007/ 2008).

In this study, the behaviour parameter 'breed' increased to a maximum of 35 % of all sessions **during** visitor stay at 5 m, while increases **post-visit** reached their maximum (31 %) during the third post-visit interval (5-6 min), again tallying with observations reported by Holmes (2007) and Holmes & al. (2005/ 2006, 2007/ 2008). With respect to visitation, definitions employed by other studies proved incomparable to the one used here (e.g. Hockey & Hallinan 1981: number of birds incubating; Fowler 1999: brooding chicks).

Increased agonistic behaviour **during** visitation was found in 56 % (59 of 105) of African penguins, *Spheniscus demersus*, approached by 3 people to within 5 m (Giese & al., unpubl. data). In Magellanic penguins, *S. magellanicus*, Fowler (1999) encountered increased agonistic behaviour during approach by a single person to within 1 m in 50 % (10 of 20 penguins from an 'isolated area' with very scarce previous exposure to researchers), 25% (5 of 19 penguins from a 'study area' with more common but infrequent previous exposure to researchers), and 5 % (1 of 20 penguins from an area frequented by tourists), respectively. Most studies did not find (e.g., Holmes 2007, for King, Royal, and Gentoo penguins, resp.) or did not examine (e.g., Fowler 1999) increased agonistic behaviour **after** visitation.

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[27] Additionally, numbers of birds remaining in the colony dropped to 85 adults and 11 chicks, respectively.

[28] incubation

[29] chicks hatched, one parent present at all times (vs. post-guard/ crèche stage: both parents foraging)

In THIS STUDY, increased agonistic activity had its maximum **during** visitor stay at 3 m (33 % = 13 of 39 sessions), and even there, it was lower than that observed for African penguins approached to 5 m, and 'isolated area' Magellanic penguins approached to within 1 m. Visual appraisal additionally found agonistic activity to be increased (as compared to pre-visit) in the first and third **post-visit** interval (19 % = 8 of 42 sessions and 18 % = 7 of 38 sessions, resp.), during which proportions closely resembled those calculated for the visiting stage 'visitor approach to 5 m' (+18 % = 7 of 39 sessions).

More detailed studies focusing specifically on agonistic behaviour might resolve whether the discrepancy between response consistencies (THIS STUDY vs. literature results) was primarily due to genus-differences (*Spheniscus* vs. *Pygoscelis*), to differences in environment (as found by, e.g., WAAS 1990 in Little blue penguins, *Eudyptula minor*), to sampling methods (counting agonistic acts per minute vs. time spent performing agonistic acts), to differences in experimental conditions, or to differential previous exposure to human presence.

Increased occurrence of headshakes (AINLEY 1974, GIESE 1998) and ruffle-shakes (AINLEY 1974) **during** human presence has been reported for Adélie penguins, *Pygoscelis adeliae*.

While transcribed separately in THIS STUDY, headshakes and ruffle-shakes were analysed jointly (subsumed under 'headshakes'). Occurrence of headshakes was likewise found to increase **during** human visitation, with maximum values observed during visitor stay at 3 m (44 % = 19 of 43 sessions) and during the first **post-visit** interval (44 % = 20 of 45 sessions). With respect to magnitude (How much?), values presented by AINLEY (1974) and GIESE (1998) both show pooled mean within-bird increases discussed below (following section), but it seems safe to assume that increases reported by AINLEY (1974: n=499 birds in 15 colonies) do not solely concern certain individuals exhibiting more headshakes while others remained unresponsive.

Posture changes ('getting up') in response to human **approach/ presence** have been observed for Adélie penguins, *Pygoscelis adeliae* (AINLEY 1974, GIESE 1998), and were likewise found to occur in other species (e.g., Emperor penguins, *Aptenodytes forsteri*: BURGER & GOCHFELD 2007; Magellanic penguins, *S. magellanicus*: YORIO & BOERSMA 1992; Humboldt penguins, *S. humboldti*: ELLENBERG & al. 2006; African penguins, *S. demersus*: GIESE & DEVILLIERS 2004, HOCKEY & HALLINAN 1981, VANHEEZIK & SEDDON 1990). BURGER & GOCHFELD (2007) reported that upon noticing people (tourists standing close to an Emperor thoroughfare; human group size: 2-60), Emperor penguins usually changed posture (stopped tobogganing and stood up). GIESE & DEVILLIERS (2004; 3 approachers) found that in African penguins 25 % of birds[30] on exposed nests (all but one were incubators) abandoned during approaches.

The Adélie penguins studied by GIESE (1998, single visitor) responded far more extremely than the ones observed in THIS STUDY[31], with human approach to 5 m causing adoption of an upright posture in 68% (n=25 outfitted with ECG transmitters) and 63 % (n=23 free of equipment) of penguins, respectively. As GIESE stated, these penguins had been chosen precisely because they had never been visited by commercial tourists and the site had been relatively free of visitation by scientists. While the Adélie penguins in THIS STUDY were likewise unaffected by commercial tourism (SSSI regulation) and were not subjected to regular visitation by scientists or station personnel either, they did encounter humans on the beach (scientists working on other projects) so that the human shape itself might have constituted less of a 'novel object' to them than to GIESE's study birds.

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[30] n=105 for birds on exposed, semi-sheltered and sheltered nests together; abstract does not offer information on numbers for each nest-type

[31] in which posture changes were encountered in 39 % of all sessions during visitor stay at 5 m

6.2.2.2.5 Focal Animals – Topography: Changes in Behaviour s.l. Detected by Quantitative Comparisons

In this study, quantitative comparison of prevalence of the different behaviours/ postures found significant differences between pre- and **during**-visitation (particularly with respect to the behaviour systems of resting and vigilance, headshakes, and the posture ‘prone’). ***Single-key values*** (difference in period medians, DiM; median of differences, MoD) were mainly able to detect differences in resting and vigilance behaviour, while ***range***-values (span from min. to max.) showed great fluctuations for all behaviours, and pointed to distinct individual responses partly dependent on behavioural repertoire exhibited prior to visitation. The cessation of human presence did not generally result in complete recovery **after** visitation. The latter finding was only partly reflected in MoD-value, whereas range-values for all behaviours were again substantial. This result suggested a persisting individuality of post-stimulus responses and, ultimately, recovery.

In Adélie penguins, *Pygoscelis adeliae* (n=25), Giese (1998) measured vigilance as an event (number of head turns performed per minute), and found significant differences (mean number of acts per minute pre-visit: slightly below 4; during-visit at 5 m: slightly below 8[32]) between the periods of pre- and **during-visit**. The paper does not provide information with respect to response levels maintained in the **post-visit** period. Gentoo penguins, *P. papua*, approached by 1 visitor, and those approached by a group of 5 visitors exhibited significant behaviour differences as compared to before the approach, primarily heightened vigilance (Holmes 2004; exact values not provided in abstract). Gentoo penguins studied by Nimon (1997) remained alert (head raising, turning, orienting; measured as state) throughout a ‘brisk-approach-visit’ by a single person, and Holmes (2007) reported a significant increase in mean number of vigilance events per minute (180°-head turns and instances of neck extension, difference analysed by paired t-tests; pre-visit: 12.59±9.85 events/min) for Gentoos (n=24) **during** visitation, as well as during the first five minutes **after** visitation. With respect to King penguins, *Aptenodytes patagonicus* (n=26), the same paper stated significantly increased vigilance (same definition, same analysis; pre-visit: 2.05±0.81 events/min) **during**, but not **after** visitation. In Royal penguins, *Eudyptes schlegeli* (n=26), Holmes & al. (2005) found a six-fold increase in vigilance **during** pedestrian visitation (to a mean of approx. 18 acts/min; max. above 20 acts/min, cf. figs. 4a and 6 in publication). They also stated that vigilance levels in Royal penguins remained significantly elevated during a 3 min **post**-approach-period. Holmes (2007) and Holmes & al. (2007/ 2008), likewise observed higher levels of vigilance (definition and analysis as described for Gentoos; pre-visit: 1.05±0.39 events/min) for Royal penguins (n=24) **during** visitation; in contrast to Holmes & al. (2005), however, they did **not**[33] find statistically significant differences between pre- and **post-visit** vigilance behaviour.

This study measured vigilance as a state, rather than an event (proportion of time spent vigilant per period). Results of ***DiM-values*** (difference in period medians, focusing on period differences across all focal birds; pre: 28 %, range: 2 % to 82 %; during: 64 %, range: 28 % to 9 %; post: 34 %, range: 5 % to 88 %) are slightly more pronounced than mean values presented by Giese (1998, from approx. 4 acts/min to approx. 8 acts/min; no post-visit value presented); for better comparison, the respective arithmetic ***mean*** values from this study, however, would amount to 32 % (pre-), 64 % (during-), and 38 % (post-), which tallies well with Giese’s finding of an **approximate doubling of vigilance level** from pre- to during-visitation.

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[32] exact values not mentioned; approximations as measured from fig. 1 in publication

[33] Results reported do not specify whether this discrepancy was due to different individuals (but both studies conducted on Macquarie Island, locations described as: ‘between Green Gorge and Red River’), sampling periods (for 2005: 28.10.-17.11.2001; for 2007 and 2007/ 2008: 01.12.-10.12.2001) or methods of analysis (cf. resp. publications).

Comparison of median and mean values obtained in THIS STUDY thus additionally reflects more variable vigilance levels prior to and after visitation (disparity between mean and median values), whereas **during visitation**, responses appear to have attained a **greater uniformity** which is also seen in the reduction of range.

MoD-values (median of between-period differences, focusing on response differences obtained from individual birds) indicated an increase from **pre- to during**-visit (+32 %, range: -11 % to +73 %) and a slightly less pronounced decrease from **during- to post-**visit (-31 %, range: -65 % to +18 %), resulting in a persisting increase when **pre- and post-**visitation periods were compared (+8 %, range: -35 % to +57 %).

Range-values for all periods/ between-period differences again emphasise the **limitations of averages** with respect to depicting 'reality' for individuals, indicating, e.g., **recovery** to be more quickly achieved for some and seriously delayed for other penguins.

Concerning Adélie penguin, *Pygoscelis adeliae*, comfort behaviour[34] , AINLEY (1974) found increases in rapid-wing-flaps (RWF) and both-wings-stretches (BWS) **during** human approach from 10 m (RWF: 0.002; BWS: 0.014; number of penguins responding, divided by minute and group size) to 2 m (RWF: 0.006; BWS: 0.027). Upon re-withdrawal to 10 m, occurrence of rapid-wing-flaps decreased to approximately pre-visit levels (0.001, difference not significant), whereas both-wings-stretches were observed to occur significantly less frequently than upon initial stay at 10 m (0.008). With respect to the latter finding, AINLEY (1974, p. 28) concluded that "[o]ne expects less stretching just after arousal than at rest and during arousal". GIESE (1998), in contrast, stated that no differences in comfort behaviour were detected **during** visitation.

As mentioned above (visual appraisal, key question: How many?), comfort behaviour was rarely encountered in THIS STUDY, and maximum values, rather than medians were affected **during-** as well as **post-**visitation, i.e. those birds who did engage in comfort behaviours tended to reduce them. Extensive occurrence of rapid-wing-flaps, which seem to indicate readiness for imminent departure (cf. AINLEY 1974, p. 25: "association with escape behaviour, including situations where they do not flee but flight is a definite possibility"), was not observed in THIS STUDY, which might be due to maintenance of a greater visitor-penguin distance (minimum 3 m, as opposed to 2 m in AINLEY 1974), and/or less time spent at each distance (2 min, as opposed to 5 min in AINLEY 1974).

Concerning results on changes in breeding behaviour presented HERE (i.e., concerning egg and nest manipulation, shuffling = rocking on the eggs, nest-bowl scratching), no study reporting on differences in prevalence of breeding behaviour performed (rather than breeding success or nest abandonment) was found.

In THIS STUDY, results of ***DiM-values*** (focusing on period differences across all focal birds; pre: 1 % of pre-visit period spent performing breeding behaviour, range: zero to 20 %; during: 3 %, range: zero to 18 %; post: 2 %, range: zero to 57 %) indicated an increase **during** visitation, and a less pronounced decrease **after** visitation, resulting in **incomplete recovery**. ***MoD-values*** (focusing on between-period response differences of individual birds) likewise detected increases from **pre- to during-**visitation (+0.24 %, range: -17 % to +17 %), but – in contrast to differences in (period) median – found a further increase from **during- to post-**visitation (+0.20 %, range: -15 % to +41 %),

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[34] As HOLMES and colleagues (HOLMES 2004, 2007, HOLMES & al. 2005, 2007/ 2008) subsumed breeding (nest-maintenance) and preening behaviours under the term 'self-maintenance' (whereas 'comfort' included 'yawning', 'defecating' and 'stretching', with all changes statistically n.s.), no separate values are available with respect to their findings on Gentoo, King, and Royal penguins, respectively. The same applies to NIMON (1997), who assigned these activities conjointly to the category 'comfort'.

and thus a more pronounced increase in breeding levels between **pre- and post-**visitation (+0.60 %, range: -18 % to +57 %).

The **differences between** these **key values** are suggested to signify that while relatively many penguins showed increased breeding behaviour post-visit, substantially increased levels of breeding behaviour were found in relatively few penguins, whose ‘excesses’ are more strongly neglected in the calculation of difference in (period) median values than with respect to median of (between-period) differences.

For Adélie penguins, *Pygoscelis adeliae*, Giese (1998) found agonistic events to increase from a mean of approx. 0.10 acts/min pre-visit to a mean of approximately 1.55 acts/min **during** visitor stay at 5 m, thus indicating a 14.5-fold increase. Agonistic acts in King, *Aptenodytes patagonicus*, Gentoo, *P. papua* (here: threat-display behaviour), and Royal penguins, *Eudyptes schlegeli* (Holmes 2007, Holmes & al. 2007/ 2008), were likewise found to increase significantly (no values presented) **during** visitation (from pre-visit levels of 0 acts/min, 1.76±0.74 acts/min, and 0.08±0.07 acts/min, resp.; for all: difference analysed by paired t-tests), but were not significantly different from pre-visit levels **after** the visit had terminated.

In this study, agonistic behaviours were measured as a state, rather than an event (proportion of time spent performing agonistic behaviours per period). This difference might have served to better capture time spent performing alternate or sideways stares as these do represent states, whereas the behaviours ‘point’ and ‘gape’ are more truly reflected in frequency counts. As stares and point/ gape were often encountered within the same sequence, however, state measurements were considered superior in portraying overall level of agonistic behaviour. Concerning ***DiM-values***, prevalence of agonistic behaviour was found to distinctly increase **during** visitation, from 0.90 % (of all behaviours observed during the pre-visit period; range: zero to 11 %) to 1.50 % (during-visit; range: zero to 23 %), and to remain elevated **after** the visit terminated (1.10 %; range: zero to 15 %). As expected (with a range for which the bottom threshold is immutable, and expansion thus limited to the upper level), ***mean*** values would have amounted to higher proportions (2 % pre-, 3 % during-, and 3 % post-visit, resp.). ***MoD-values*** (focusing on response differences of individual birds) indicated an increase from **pre- to during-**visit (+0.30 %, range: -5 % to +19 %) and no changes in median between either **during- and post-**visit (zero, range: -17 % to +11 %) or – interestingly – between **pre- and post-**visit (zero, range: -5 % to +15 %) periods. Again, the respective ***mean between-period difference*** values would have awarded more weight to outliers (with values for pre→dur +1.37 %, dur→post: -0.60 %, and pre→post: +0.77 %, resp.), and, together with ***range***-values for MoD, suggest a more consistent increase in response for changes from pre- to during-visitation, whereas differences between during- and post- as well as between pre- and post-visit appear to have been less consistent with respect to direction and magnitude, pointing to individual differences in post-stimulus **recovery**.

Ainley (1974) measured changes in occurrence of head- and ruffle-shakes (in 15 colonies) in terms of number of acts performed per minute (5 min at 10 m and at 2 m, resp.) and bird (total n=499 birds). Giese (1998) looked at individual birds and evaluated headshaking behaviour in terms of acts per minute (n=25 birds). Ainley (1974) found the frequency of Adélie penguin headshakes to almost double when the observer was standing at 2 m (0.113) from the colony edge after having stood at 10 m (0.058), and to decrease marginally (difference not statistically significant) after re-withdrawal to 10 m (0.103). Giese (1998) reported an increase from approx. 0.10 per minute pre-visit to approximately 0.80 per minute **during** visitor stay at 5 m; no information on performance in the **post**-visit period is provided. Additionally, Ainley (1974) observed a tripled frequency of occurrence of ruffle-shakes during visitation, followed by an almost complete **recovery** after the visitor had withdrawn (at 10 m: 0.022; at 2 m: 0.060; re-withdrawal to 10 m: 0.024).

As visitation time in THIS STUDY depended on visitor conduct (loud and fast visits being shorter than silent and slow visits due to different approach and retreat times) occurrence of headshakes (including ruffle-shakes) was measured as a proportion of time per period (i.e., divided by sum of seconds); ***DiM-values*** indicate a distinct increase **during**-visit, from zero pre-visit (range: zero to 5 %) to 0.40 % (range: zero to 3 %; respective ***mean*** values for comparison with AINLEY 1974: 0.36 % pre-visit to 0.61 % during-visit), and a reduction by half in the **post-visit** period (0.20 %, range: zero to 3 %; not reflected in the mean value: 0.60 %). ***MoD-values*** (focusing on response differences of individual birds) indicated an increase from **pre- to during-**visit (+0.20 %, range: -4 % to +3%) and a slight decrease from **during- to post-**visit (-0.06 %, range: -3% to +3 %), resulting in a persisting increase when **pre- and post-**visitation periods were compared (+0.10 %, range: -3% to +3 %). To permit more direct comparison with AINLEY (1974), respective ***mean between-period*** values are additionally provided here: They amounted to +0.25 % (pre- vs. during-), zero (during- vs. post-), and consequently +0.25 % (pre- vs. post-visit).

Magnitudes of differences between periods and **direction** of change observed in THIS STUDY thus appear to reflect those reported in previous studies reasonably well. With respect to the post-visit period, however, differences in (period) median values (DiM) seem to inadequately portray the persisting increase (as compared to pre-visit levels). Given the differential 'embracement of outliers' in the two averages (with mean-values considerably more affected by extreme responses), results point to substantial differences in post-visit responses between different individuals (also reflected in ***range***-values). This is to some extent supported by values of median (and more so by mean) between-period differences (MoD), which detect the relative absence of recovery with greater accuracy.

As for changes in posture, GIESE (1998) recorded a mean of approximately 95 % of time spent prone at a visitor distance of 30 m, and a significantly reduced mean time spent prone (above 60 %, cf. fig. 1 in GIESE 1998) **during** visitor stay at 5 m.

THIS STUDY, in contrast, found ***DiM-values*** of only -5 % (from 100 % to 95%, range: 25 % to 100 %) from **pre- to during-**visitation, followed by a median re-increase to just below pre-visit levels (post-; 98 %, range: zero to 100 %). Calculation of ***difference in mean values*** does not yield results more similar to GIESE's (from pre- to during-: decrease by -6 %, from during- to post-: increase by +2%, remaining difference pre- vs. post-visit: decrease by -4). ***MoD-values*** (focusing on response differences of individual birds) likewise showed a reduction from **pre- to during-**visitation (by -1 %, range: -67 % to +93 %), a re-increase from **during- to post-visitation** (by +0.60 %, range: -90 % to +53 %) and a MoD-value of 0 % between **pre- and post-**visitation (zero, range: -100% to +98 %).

Differences between GIESE's and THIS STUDY are again suggested to result from differential experience of humans as a 'novel object' so that with respect to **magnitude** of postural response (How much?) the same explanation applies as when looking at **consistency** of response (How many?; see previous section).

Concerning the 'exorbitant' ***range***-values found in THIS STUDY, these need to be viewed in the light of prior activity of individual penguins: Extreme values were found to be partly associated with abrupt reductions of comfort (e.g., Y6-2, 01.12.2001: from pre- = 70 % comfort to post- = zero) and/or breeding (e.g. X1-1, 23.11.2001: from pre- = 20 % breed to post- = 4 %) behaviour (pre-:

up, during-/ post-: prone), and with prolonged bouts of preening (e.g., X1-1, 26.11.2001: from pre- = 0.6 % comfort to post- = 79 %) and/or egg-manipulation (e.g., B3-1, 13.11.2000: from pre- = 8 % breed to post- = 47 %) after visitation (pre-: prone, during- and/or post-: up). While the parameter posture might serve as an ad hoc indicator of disturbance during visitation (birds getting up), it is concluded that care must be taken with respect to obtainment of and comparison to 'baseline levels' (prior to visitation), as these need to be seen in conjunction with specific behaviours performed (major feats of egg manipulation and to a lesser extent diligent whole-body preening are more difficult to achieve when prone).

Moreover, the fact that individual focal animals either interrupted longer bouts of preening or egg-manipulation **during** visitation or initiated these behaviours **after** the visit had terminated appears to merit further consideration, as it might indicate human visitation to seriously disrupt the penguins' current motivational status.

6.2.2.2.6 Focal Animals – Topography: Changes in Behaviour s.l. as Reflected in Distribution of Phases/ States

Second-by-second transcription of focal-animal behaviour[35] and subsequent identification of phases pertaining to different behaviour systems yielded insight not only into the ***composition*** (distribution of different behaviours in the course of time, might be equated with time budget), but also into the structural component underlying expression of all and each behaviour system(s). The structural component encompasses the duration and number of phases (behaviour) and states (posture), and can be thought of as the ***'syntax'*** of comportment (for HR, see discussion of Aim II). 'Syntax' alterations may affect all or selected comportment parameters, and directions of changes may be the same or different: If the 'syntax' beneath the expression of **overall comportment** is altered in the same direction, this leads to **general pattern changes** in topography (e.g., shorter phases irrespective of contents), whereas structural alteration of **selected comportment parameters** (e.g., only more shorter phases of 'rest'; shorter phases of 'rest' and longer phases of 'vigilance') need not result in general changes. **Structural alterations** are suggested to constitute an additional way in which behaviour may change; these alterations might be thought of as being more 'fundamental' than an increase/ decrease in performance in which the structure remains unaffected (e.g., fewer phases of 'rest' without changes in duration of individual phases).

No studies on this type of evaluation were found in the literature; therefore, discussion is limited to results obtained in THIS STUDY.

Examination of overall distribution of phases and states across periods of the visit revealed **changes in the 'syntax' of overall behaviour and posture**. While the shift towards shorter phase durations for behaviour[36] might appear irrelevant at first sight (an increase in number of phases assigned to the short-durations class by only +3 % pre- vs. post-visit), attention is drawn to the fact that this led to a +10 % increase in time spent on short phases, indicating a non-negligible decrease in cohesiveness of behaviour performed. Moreover, the increase in short-durations phases observed **during** visitation continued in the **post-visit** period (further increase from during- to post-visit). Spending considerably more time performing phases of short duration – with the consequence of increased frequency of switches between behaviour systems – is suggested to reflect a greater state of **general agitation** and points to persistence of impact of human visitation, which is not necessarily picked up when analysing 'amount of behaviour expressed': The sequence of, e.g.,

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[35] same applies to posture

[36] denoting behaviour s.s. (i.e., excluding posture), while the term behaviour s.l. is used if posture is included

‘3 s of rest, 5 s of vigilance, 3 s of rest, 6 s of vigilance, 3 s of rest’ receives the same additive value (time budget) as ‘9 s of rest, 11 s of vigilance’, but the latter is – presumably – more restive than the former. With respect to posture, the trend was approximately the opposite, with an increase in medium state durations **during**, and in long state durations **after** visitation.

During and after visitation, focal animals thus appeared to be more ready to ‘stay put’ posture-wise, but while maintaining that posture, they were more inclined to switch more frequently among behaviour systems. A study quantifying the costs incurred by switches among different behaviour systems is needed to evaluate these findings in terms of energy expenditure as well as increased susceptibility to nest stone theft or predation.

Results from THIS STUDY found marked **changes in composition of behaviour and posture** both during and after visitation.

Prior to visitation, proportions[37] of total phase/state number (TPN/ TStN) were lower than proportions of total phase/ state time (TPT/ TStT) only with respect to the parameters ‘rest’ and ‘posture_prone’; they were identical for the parameter ‘comfort’, and higher proportions of numbers than time were encountered for all other parameters. **During** visitation, decreases particularly concerned the parameters ‘rest’ (TPN: -10 %, TPT: -40 %) and ‘posture_prone’ (total state number, TStN: -14 %, total state time, TStT: -42 %), and to a much lesser extent comfort behaviour (TPN: -0.82 %, TPT: -2 %). Increases were particularly prominent as regards the parameters ‘vigilance’ and ‘posture_up’ (s.b.), and also found in the parameters ‘interruptions s.l.’ (TPN: +7 %, TPT: +2 %), ‘agonistic’ (TPN: +2 %, TPT: +1 %), and ‘breed’ (TPN: +0.93 %, TPT: +0.31 %).

During visitation, a substantial **switch in ‘number-time-relation’** was observed in the parameter ‘vigilance’ (pre-visit TPN: 42 %, TPT: 29 %) for which a minimal increase in phase number during-visitation (+1 %) was accompanied by a massive increase in phase time (+37 %). A similar ‘switch’ was also found in the parameter ‘posture_up’, with 48 % of all states resulting in 17 % of time spent ‘up’ prior to visitation, while during visitation, an increase of +14 % in phase number resulted in an increase of +42 % in phase time. With respect to these parameters, human visitation thus already pointed to a pronounced structural alteration of phases (within-parameter changes in ‘syntax’, s.b.) not as readily apparent in the other parameters.

Concerning the parameter ‘rest’, **during-**visit proportions were reduced by about one third with respect to TPN and by approximately two thirds with respect to TPT. As for posture ‘prone’, loss of a quarter of all phases in terms of TStN resulted in a reduction by half of TStT. While structural alterations are thus not as quite as discernible as in ‘vigilance’ and ‘posture_up’, differences between magnitudes of decrease point to differential losses, with phases of longer duration more affected than those of shorter duration; this aspect will be further discussed below.

As regards the parameters ‘breed’, ‘agonistics’, and ‘interruptions s.l.’, greater increases in TPN than in TPT were found **during** visitation, so that these can be seen as definite **contributors to** the increase in **scattered behaviour** detected by visual appraisal (s.a.). The increase in within-phase ‘impurities’ may likewise have added to that impression.

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[37] Analysis of proportions of time spent performing phases assigned to each of the behaviour systems (Aim I, section 6.2.2.2.6) is different from analysis of proportions of time spent performing elements assigned to each behaviour system (Aim I, section 6.2.2.2.5) in that the latter makes no distinction between isolated elements performed against the background of another behaviour system (e.g., a vigilant head turn during prolonged resting behaviour) and longer stretches of time spent in a given system. Due to brevity of minimum phase duration (3 s), however, differences are not pronounced. To additionally permit detection of isolated elements, the degree of ‘impurity’ of phases was examined as well.

After visitation, a **reversal of response directions** was generally observed, with the exception of the parameter 'breed' which continued to increase and for which TPT increased more than TPN, thus indicating more as well as longer phases.

In terms of **recovery**, the **persisting change in composition** observed post-visit (less resting phases, more vigilance and breeding phases, more interruptions, slightly more phases of comfort and agonistic behaviour) supported the impression of a **'continuing state of agitation'**, mainly expressed by heightened vigilance and breeding behaviour, but to a lesser extent also by other activities (pursued less frequently and/or by fewer individuals). It also suggested a waning of structural alterations with respect to the parameters 'vigilance' and to a lesser extent for 'posture_up', but did not yet permit conclusions concerning the remaining parameters.

Examination of **within-parameter changes in 'syntax'**, (phase distributions across short-, medium-, and long-durations classes within individual parameters, i.e., category phase/ state number and time, CPN, CPT; CStN, CStT) demonstrated vigilance to be the only behaviour for which distribution post-visitation was approximately the same as that observed prior to visitation, even though more overall time was devoted to vigilance (+6 %). The **structural alteration** observed during visitation thus almost completely disappeared, with 'more overall time' indicating persisting within-class or even within-subclass shifts towards longer durations. While quantitative comparison of vigilance levels in individual sessions (see range-values discussed above, pre- vs. post-visit: from decrease by -35 % to increase by +57 %) had shown substantial inter-individual differences with respect to recovery in terms of time spent vigilant, a **'structural recovery'** on the class- (albeit sometimes not subclass-) level occurred in the majority of sessions. In other words: While the birds tended to spend more time vigilant even after the visitors had left, they did so in a similar manner as prior to visitation.

This capacity of 'bouncing back' in terms of structure was not shared by the other parameters, which either exhibited a far slower return (e.g., 'rest', with medium- as well as long-durations phases still fewer than pre-visit, but more than during-visit) or showed alterations even more pronounced than during visitation (e.g. 'agonistics', with shifts occurring only within the short-durations class during-visit, but more phases assigned to the medium-durations class post-visit).

6.2.2.3 Differential Perception of Disturbance Stimuli

Directions of response were generally found to be comparable to those reported in the literature (e.g., AINLEY 1974; BURGER & GOCHFELD 2007; CULIK & al. 1989, 1990a; DEVILLIERS & GIESE 2004; GIESE 1998; HOLMES 2004, 2007; HOLMES & al. 2005/ 2006, 2007/ 2008; NIMON 1997; WILSON, R.P. & al. 1991; VANHEEZIK & SEDDON 1990); deviations in **magnitude** of response could in some cases be explained by differences in experimental/ study design and/or recording method, but remained inconclusive in others.

Differential perception of disturbance stimuli presented to different birds in different studies is proposed as a possible answer to these disparities: According to BOISSY (1995), GRAY (1979) classified **fear-producing stimuli** into five (non-mutually exclusive!) subdivisions:

1. stimuli that represent dangers which are part of the evolutionary history of the species,
2. stimuli that acquire valence through increased intensity (e.g., velocity of speed, volume of noise),
3. stimuli that acquire valence because of novelty,
4. stimuli that acquire valence after an individual learning process, and
5. stimuli that acquire valence from interactions with conspecifics, thus representing a social learning context.

It is important to realise that these subdivisions do not represent ‘pure traits’, but rather try to get a grip on different traits pertaining to a given stimulus; consequently, any stimulus may comprise several of these traits, although one or a few of these might be responsible for the predominant quality (i.e. a stimulus may predominantly constitute a novelty, but additionally be reinforced by social learning).

Similarity of **direction** of responses is suggested to result from the fact that penguins generally perceive **humans as ‘predation-free predators’** covered by the stimulus trait ‘evolutionary history’ (e.g., Beale & Monaghan 2004a; also see chpt. 2 in this thesis), with the perception at least partly linked to ‘looming quality’ of humans over penguins. Several studies (e.g., Nimon 1997; Giese 1998) reported lesser responses to crouching humans – unfortunately mitigated by the fact that these humans generally had to stand up again at some stage, thereby producing a pronounced reuptake of response. The ‘social learning’ context might be another stimulus trait favouring similarity of direction of response, at least within the same colony. In this study, particularly the behaviours of vigilance and resting appeared strongly influenced by social facilitation, which might be thought of as a precursor to social learning.

The stimulus trait ‘evolutionary history’, however, might also produce disparity with regard to **intensity** (if compared qualitatively) *or* **magnitude** (comparison of – comparable – measurements) of responses between species/ populations: Ellenberg et al.’s study on Humboldt penguins, *Spheniscus humboldti* (2006), provides evidence for a rather rapid species response to ‘unnatural selection’ in the form of actual human predation. Humboldt penguins – unlike their congeners, Magellanic penguins, *S. magellanicus* – have been hunted by coastal human communities for the past 11,000 years, and this species was found to respond far more extremely to human visitation than many others. Additionally, Humboldt penguins exhibited a very limited capacity to habituate, which Ellenberg & al. (ibid., p. 104) attributed to the possibility of more tolerant individuals (respectively the offspring thereof) having been lost from the wild population (also see Cobley & Shears’ 1999 report on Gentoo penguins’, *Pygoscelis papua*, observed lack of responses to human visitation in that particular population).

Apart from that, however, **differential individual perception** of stimuli presented is proposed to add to differences in response intensity or magnitude. Within this context, the ‘exherent’ (with the verbal invention referring to dependence on individual, viz., penguin, perception of stimulus, rather than actual, i.e., inherent, quality of stimulus itself) traits of valence acquisition of stimulus by individual learning, degree of novelty, and perceived stimulus intensity attain greater importance, as these to a large extent cannot be influenced by experimental and/or study design.

For cases in which a whole population (or colony or breeding group) subjected to a given experimental treatment differs from another population (do.) subjected to approximately the same treatment (e.g., differences between birds getting up in Giese’s 1998 study and this study), attribution of the difference to a given stimulus trait (rather than to experimental design) will sometimes become more probable; as mentioned above (Aim I; section visual appraisal), it appears reasonable to postulate difference in perceived novelty of stimulus with respect to humans in this example.

6.2.3 Aim II: Impact of Human Visitation on Heart Rate

H_0: There will be no differences in heart rate before, during, and after human visitation.

- H_{1A}: Heart rate during visitation will differ from heart rate before visitation.
- H_{1B}: Heart rate during visitation will differ from heart rate after visitation.
- H_{1C}: Heart rate after visitation will differ from heart rate before visitation.

Recapitulation: The difference between **pre- and during-**visitation is considered to reflect the immediate effect of visitation, while the difference between **during- and post-**visitation is suggested to shed light on the focal animals' continuing/ waning response after withdrawal of the stimulus. The difference between **pre- and post-**visitation thus gives an indication as to the extent to which the animals have managed or failed to recover during the post-visit period.

6.2.3.1 Conclusions – Between-Period Differences in Heart Rate

With respect to absence of between-period differences in heart rate, H_0 was successfully refuted.

In conclusion, human visitation elicited substantial changes in incubating Adélie penguins' heart rate, both during the visit itself and after visitation. Alterations were observed with respect to **consistency** (numbers of penguins exhibiting increased heart rate), as well as in the **composition** of heart rate (distribution of phase durations among the categories below, within, and above mean resting heart rate ±2 SD), and in terms of changes in **'syntax'** (overall structure of heart rate; structure within individual categories).

With respect to **magnitude**, increases in a number of descriptive statistical parameters (mean, standard deviation, maximum, range) as well as a greater variability of heart rate during- and post-visitation (as compared to pre-visitation), were distinctly different from changes in 'baseline' heart rate examined in successive 10 min-intervals.

Direction as well as magnitude of general response (increase) tallied well with values found in **previous publications**, but for some penguins, heart rate responses were non-existent or inverse.

Comparison of heart rate changes during **disturbance** to **'voluntary' physical exertion** (diving) suggested the different qualities of stimuli experienced rather than different regulatory pathways to be responsible for the apparent inability to regulate heart rate in the face of human disturbance. The stimulus trait 'novelty' (including 'unpredictability' and 'uncontrollability') is assumed to attain the greatest relevance in this context. Next to species- and perhaps population-differences (evolutionary history) in responsiveness, varying degrees of 'novelty' are additionally proposed to explain the differential heart rate responses to human disturbance reported in the literature.

Following, results pertaining to the question of between-period differences in heart rate will be discussed.

6.2.3.2 Placing Results Obtained into Context

6.2.3.2.1 Focal Animals – Topography: Changes in Heart Rate Detected by Visual Appraisal

THIS STUDY found heart rate to **increase in most penguins** (80% of all sessions) during visitation and to decrease again after the visitors had left. Heart rate responses of similar cohesion (i.e.

concerning all or most of the birds subjected to visitation) were likewise reported by other authors for Adélie, *Pygoscelis adeliae* (Giese 1998), as well as other penguins (e.g., African, *Spheniscus demersus*, DeVilliers & al. unpubl. data; Humboldt, *S. humboldti*, Ellenberg & al. 2006; Royal, *Eudyptes schlegeli*, Holmes & al. 2005). In contrast, Nimon (1997) emphasises that in her study not all Gentoo penguins, *P. papua*, which were approached by a single, well-behaved visitor responded with increased heart rate, and if they did, changes consisted of brief (10 s to max. 30 s) increases. Furthermore, in Snares crested penguins, *Eudyptes robustus*, Ellenberg & al. (2004) detected no heart rate response to close human proximity outside the colony, and even upon within-colony approach to 2 m, some individuals did not exhibit a significant heart rate change.

In this study, focal-animal heart rate was more sensitive to **stimuli moving** towards/ away from the birds than to stimuli remaining at a stable distance, with greatest changes (highest proportional value for increased heart rate) assigned to the visiting stage of ‘visitor approach to 5 m’, and second highest value to the stage of approach to 3 m. Most published studies (including Nimon 1997) also found that moving stimuli generally elicited a stronger heart rate response than still ones. Interestingly, movement is often reported to result in heightened response level irrespective of direction, i.e., the penguins responded to the movement of visitors kneeling/ crouching down as well as to that of getting up, and elevations in heart rate were observed during visitor retreat as well as visitor approaches. It would thus appear that any movement increases the unpredictability of a given stimulus and is therefore liable to elicit a stronger response (also see section 6.2.6).

In the penguins examined in this study, increased heart rate also occurred **without overt behavioural changes**, mainly during approaches to 15 m and 5 m. Some previous studies likewise reported heart rate changes in conjunction with apparently unaltered behaviour (e.g. for Adélie penguins, Wilson, R.P. & al. 1991, Giese 1998; for Humboldt penguins, Ellenberg & al. 2006). With respect to approaches to 5 m as well as to 3 m undertaken in this study, this is mainly attributed to the fact that approach time was very short compared to visitor stay at a given distance; therefore, behavioural changes were less likely to be assigned to these visiting stages than a ‘quicker-to-achieve’ increase in heart rate. Concerning the substantially longer approaches to 15 m, however, heart rate responses might indeed constitute a precursor to behavioural responses.

Taking this argument further, behavioural responses appeared to some extent to supersede heart rate responses: As early as 1979, Duncan & Filshie found tachycardiac (i.e., increased heart rate) responses in caged hens subjected to human approach to be longer-lasting in a strain of birds deemed ‘docile’ due to expressing little behavioural changes.

In this study, a greater proportion of penguins responded with heart rate elevations during approach to 5 m (in 80 % = 20 of 25 sessions) than to 3 m (in 62 % = 16 of 26 sessions), and proportions during visitor stay at 5 m (in 45 % = 13 of 29 sessions) exceeded those at 3 m (42 % = 10 of 24 sessions). In contrast, decreases in resting behaviour, as well as increases in breeding, vigilance and agonistic behaviour, were more prominent during visitor approach to 3 m than to 5 m, and with the exception of breeding behaviour, also more prominent during visitor stay at 3 m than at 5 m. While heart rate responses in this scenario would be interpreted as ‘surprise’/ ‘shock’ responses, behavioural reactions represent ’taking overt action’, which in turn might be perceived as partially regaining control of – and thereby better coping with – the situation ‘at flipper’. In this context, it seems particularly interesting that Ellenberg & al. (2006, p. 101) reported Humboldt penguin heart rate responses elicited by natural stimuli to return to resting heart rate range “within seconds”, whereas recovery from human-induced responses (approach by a single person to within 2 m of the nest-site) needed “up to half an hour”.

The **'irregular pattern' of heart rate increases** observed in the post-visit period (highest value in first, second highest value in fourth interval) is suggested to represent a relative recovery which pointed to persisting 'excitability' of some of the birds after cessation of human visitation. Topography charts (see appendix 5.3.1-1) indicated that this 'excitability' was not usually linked to directly observable changes in natural stimuli (like increases in numbers of conspecifics or increased presence of predators) so that a heightened state of 'apprehension' as a consequence of human visitation is postulated.

6.2.3.2.2 Focal Animals – Topography: Changes in Heart Rate Detected by Quantitative Comparison

Analysis of variation in parameters of descriptive statistics presented in chapter 5.3.2.2 differed from heart rate analyses of previous publications in that the **entire pre-visit period** was taken into account (by integrating natural fluctuations, rather than comparing during-visit heart rate to pre-visit *resting* heart rate levels only). A further difference pertains to values used in the analyses, with other publications presenting beats-per-minute values, while THIS STUDY used **values-as-counted** (20 s counting-intervals) thereby avoiding extrapolation bias and minimising the effect of potential counting errors (section 6.2.3).

Despite these differences, maximum increases **during visitation** constituted up to 175 % of pre-visitation heart rate, while the highest mean increase peaked at 195 % pre-visit. The former value approximately equates that reported by WILSON, R.P. & al. (1991, n=1 penguin), while the latter substantially exceeds that found by GIESE (1998; 153 %; mean of means, n= 25 penguins), but is close to the magnitude ELLENBERG & al. (2006, 198 %; n=17 penguins) calculated – albeit again as a mean of means – for Humboldt penguins, *Spheniscus humboldti*.

Some Adélie penguin individuals in THIS STUDY thus exhibited a heart rate response similar to a species considered extremely timid due to persisting predation pressure by humans. The majority of mean increases in THIS STUDY (12 of 29 sessions; for median increases: 11 of 29 sessions) were found to lie between 105 % and 134 % of mean pre-visit heart rate, indicating that even if the complete heart rate record prior to visitation was taken into account (irrespective of natural disturbances or level of activity), during-visit heart rate still exceeded pre-visit heart rate.

Moreover, the respective values for **'baseline' sessions** (2^{nd} 10 min-interval of sessions during which penguins were subjected to natural but not human disturbance) never constituted more than 124 % of heart rate exhibited in the 1^{st} 10 min-interval, and elevations occurred in fewer 'baseline' than 'visited' sessions (for the former: mean as well as median: 6 of 37 sessions). Furthermore, deviations did not leave the ±5 % boundary in the majority of 'baseline sessions' (27 and 25 sessions within 95 % to 104 % pre-visit heart rate for mean- and median-values, resp.), indicating heart rate responses to human visitation to by far exceed naturally occurring fluctuations.

Looking at entire pre-visit records provided the additional advantage of being able to quantify changes in standard deviation and range, thus permitting period comparison of changes in heart rate variation. THIS STUDY demonstrated substantial alterations (predominantly increases; SD: 24 of 29 sessions; range: 22 of 29 sessions) in both statistical parameters from pre- to during-visitation, which to a slightly lesser extent were still detectable when pre- and post-visit values were compared (persisting increases in 14 of 29 sessions for both parameters). As proposed with respect to behavioural changes (see section 6.2.2), this finding is suggested to point to **increased agitation** which is derived from visitation and is slow to wane during the post-visit period.

6.2.3.2.3 Focal Animals – Topography: Changes in Heart Rate as Reflected in Distribution of Phases/ States

Findings with respect to changes in phase durations were based upon the distinction of three heart rate categories, viz., below, within, and above mean resting heart rate ±2 SD (for short RHR), with RHR ±2 SD constituting the tolerance band accepted as containing naturally fluctuating heart rate. After having demonstrated heart rate changes beyond those found outside human visitation (previous section, Quantitative Comparison), analyses of distribution of phases thus followed the procedure outlined in other studies (e.g., Neebe & Hüppop 1994, Ellenberg & al. 2006, 2009) by using **RHR obtained prior to visitation** instead of the entire pre-visit record.

Results on phase durations indicated the generally greater variation in heart rate discussed above to be additionally reflected on the structural level ('syntax'): An **overall tendency towards shorter phases** was encountered **during** visitation, and this trend further increased **after** the visit had terminated.

Definition of a **tolerance band** has been previously used to distinguish heart rate *elevations* from natural *fluctuation* (s.a.), but not to examine changes in phase durations resulting from the definition. Additionally, none of the papers mentioned the extent to which heart rate fell below the tolerance band, which might either mean that it never did, or, alternatively, that this type of deviation was considered irrelevant as compared to findings on excitation.

In this study, **composition** of heart rate (i.e. distribution among the categories) changed under human visitation: Phases in the category 'below' did not become more (total phase number almost unchanged), but considerably longer **during** visitation, whereas between-category switches (from 'within' to 'above') resulted in both more and longer phases assigned to the category 'above'. For some birds[38], at least, heart rate changes did not follow the pattern usually reported for responses to disturbance. Nor did these findings tally with 'cyclical' changes (spontaneous, internally mediated increases in heart rate at regular intervals) proposed by Nimon (1997). For **each of the categories** (below, within, above RHR ±2 SD) the structure of focal-animal heart rate remained distinctly different from pre-visitation in terms of **structure** (within-parameter 'syntax'): The general 'syntax' trend towards shorter phases already discussed was found to be predominantly due to between-class switches of phases pertaining to the category 'within' (from long- and medium-durations classes to the short-durations class). Phases in the category 'above' (and to a lesser extent those assigned to the category 'below'), in contrast, tended to be longer than observed prior to visitation.

6.2.3.3 Heart Rate during Disturbance vs. Diving Bradycardia

> "As well as the selective vasoconstriction, there is also a **reduction in heart rate** during the period of submersion, which causes a reduction in cardiac output of similar magnitude. This reduction in cardiac output tends to match the increase in peripheral resistance so that there is little or no change in central blood pressure. The so-called 'diving bradycardia' is often taken as being indicative of the other physiological and metabolic events which have been shown to occur during forced submersion." (Butler 2004, p. 298; boldface added by this author)

Diving comes naturally to penguins, but nevertheless constitutes a considerable physical exertion. Responses to disturbance, on the other hand, may be considered an emotional exertion. A comparison of heart rate responses to these two challenges thus seemed worthwhile.

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[38] Diligent perusal of individual sessions revealed these values to almost exclusively come from FAs-X, and mainly from FA X2-1, indicating individual responses rather than a general pattern.

Studies and reviews on penguin physiology, particularly those investigating changes in **physiology during diving** (e.g., BUTLER 2000, 2004; KOOYMAN & al. 1992; MEIR & al. 2008; PONGANIS & KOOYMAN 2000, SATO & al. 2002) have presented evidence for an astonishing capacity to regulate physiology, including heart rate, during physical exercise. With respect to heart rate, the term ‘regulation’ is here used to refer to the fact that during the dive itself, heart rate was found to be only slightly higher[39], slightly lower[40], or even considerably lower[41] than that reported for penguins at sea but not diving, or even lower than resting heart rate on land (during surface time on the water, heart rate is generally higher than on land due to increased metabolism in low water temperatures). BUTLER (e.g., 2004) has suggested temperature decreases in selective body parts (e.g., feet) to aid reducing energy requirements, while HANSEN & RICKLEFS (2004) consider a decrease in diving metabolic rate caused by reduced buoyancy resulting from compression of air in the respiratory system and feathers sufficient to explain the findings (but see BUTLER 2004).

Given the penguins’ capacity to regulate locomotor heart rate, it is at first sight rather puzzling that the majority of **disturbance-related penguin studies** including THIS STUDY, report significantly increased heart rate for Adélie and other penguins (e.g., CULIK & WILSON, R.P. 1991, GIESE 1998, and WILSON, R.P. & al. 1991, for Adélie, *Pygoscelis adeliae*; NIMON 1997, NIMON & al. 1995, for Gentoo, *P. papua*, visited by a ‘careless’ person; DEVILLIERS & al. unpubl. data and DEVILLIERS & GIESE 2004, for African, *Spheniscus demersus*; ELLENBERG & al. 2004, 2006, for Humboldt, *S. humboldti*; ELLENBERG & al. 2009, for Yellow-eyed, *Megadyptes antipodes*; HOLMES & al. 2005, for Royal, *Eudyptes schlegeli*)[42]. In some of these investigations, increased heart rate was found to persist over longer stretches of time, while other studies observed elevations limited to stimulus presence or even more transitory, e.g., only during initial presentation (appearance) or only during changes in nature of stimulus (cf. trait ‘intensity’: crouch, then stand; stay motionless, then move).

The discrepancy between the extent of heart rate changes in disturbed and diving penguins might at first suggest different regulatory mechanisms for ‘emotionally’ vs. locomotor-mediated changes in heart rate. SATO & al. (2002, p. 1189) for instance, found King (*Aptenodytes patagonicus*) as well as Adélie penguins to regulate their air volume to “optimize the costs and benefits of buoyancy”. FROGET & al. (2004) reported King penguin heart rates to reflect anticipation of both submersion and re-emergence (increase before dive pattern change).

If control of and influence on internal body processes are ‘a given’ for penguins with respect to physical exertion, why do they fail to effect this control during emotional exertion?

The answer to this question is suggested to be connected to the **nature of the stimuli** concerned: These appear to be far more ‘penguin-controllable’ (and -controlled) during physical activity, whereas disturbance stimuli might be perceived (by the penguins) as being unpredictable, uncontrollable, ‘novel’ and/or inescapable. This supposition is to some extent supported by the differential responses observed during disturbance.

As discussed above for behavioural responses, it is likewise suggested that a greater weight might have to be awarded to the stimulus traits, particularly to the co-factor of ‘novelty’ (including

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[39] e.g., CULIK 1992, for Adélie penguins, *Pygoscelis adeliae*

[40] BEVAN & al. 2002, for Gentoo penguins, *P. papua*; BUTLER & WOAKES 1984, for Humboldt penguins, *Spheniscus humboldti*; GREEN & al. 2002, for Macaroni penguins, *Eudyptes chrysolophus*

[41] FROGET & al. 2004, for King penguins, *Aptenodytes patagonicus*; MEIR & al. 2008 for Emperor penguins, *A. forsteri*

[42] As mentioned with respect to behaviour, Snares crested penguins, *Eudyptes robustus*, appear to be a notable exception from this (ELLENBERG & al. 2004, abstract text), with no measurable heart rate response in some of the penguins examined, even “when researchers entered a colony during a direct experimental approach to within 2 m”.

‘unpredictability’ and ‘uncontrollability’), but also to species- and perhaps population-differences. Boissy (1995, p. 168) states in his review on fear and fearfulness in animals:

> “Exposure of an animal to *novelty* is one of the most potent experimental conditions leading to a negative emotional response. […] Novelty can be classified as a collative variable because the recognition of any stimulus situation as being novel requires a comparison with events that have been experienced in the past.”

6.2.4 Aim III: Extent of Individuality (Coping Strategies)

H_0: There will be no inter-individual differences in penguin behaviour s.l. and/or heart rate during disturbance.

- H_1: Interindividual differences in behaviour and/or heart rate will be present during disturbance.

> “In most ecological studies differences in conspecific individuals are treated as variation around an adaptive mean. However, individual variation in behaviour and physiology is a driving force for natural selection: pressures that act on individual fitness cause differences in reproductive success and survival.” (Ellenberg & al. 2009, p. 293)
>
> „[…] I attempt to classify these coping responses into four general coping strategies. I suggest that these coping strategies have been shaped by evolution as adaptations to different types of aversive situations with which animals are confronted in a natural environment.“ (Wechsler 1995, p. 126)
>
> “Each individual animal has several alternative methods of trying to cope with adversity and individuals differ in the methods which they favour.” (Broom 1988, p. 16)

6.2.4.1 Conclusions – Individual Differences (Coping Strategies)

With respect to absence of inter-individual differences during disturbance, H_0 was successfully refuted.

In conclusion, considerable inter- and intra-individual differences were observed in the penguins studied, both outside and during human visitation. **Inter-individual** differences concerned response levels (intensity) and response ‘preferences’ (behaviour vs. heart rate; different behaviour systems) that could not be attributed to differential severity of visiting regimes or daily weather conditions, but might have been effected by micro-site (location within colony, e.g., inter-nest distance), age/ breeding experience, differential perception of stimulus (‘novelty’), or personality/ character/ temperament. Moreover, currently not incubating conspecifics exhibited various reactions (none, stop, move away, move into colony) during human visitation.

In addition, **intra-individual** differences in individuals became apparent, indicating that caution must be taken in attributing disturbance-sensitivity only to certain behaviours (which might not be exhibited by all penguins all of the time). Intra-individual differences are suggested to reflect ‘general state of being’ prior to visitation, which is thought likely to be influenced by behaviour predominantly engaged in, and/or differential pre-visit subjection to predatorial or conspecific disturbance stimuli, and which was found to modulate behaviour responses during as well as after visitation.

Attention is drawn to the importance of including the aspect of individuality when developing tenable, effective concepts of conservation. Furthermore, inter- as well as intra-individual differences need to be taken into account when formulating guidelines for human comportment. The Modulation Model for Individual Response Differences presented in section 6.3 will attempt to summarise influences likely to effect these differences.

Following, results pertaining to the question of extent of penguin individuality in response to human visitation will be discussed.

6.2.4.2 Placing Results Obtained into Context

This study found only a very moderate correlation between heart rate and vigilance (max. r^2: 0.112), and heart rate and vigilance were uncorrelated in about half of the birds examined. This result suggests that **vigilance and heart rate do not necessarily correspond** (in the literal sense of the word). A number of explanatory possibilities spring to mind; most of them relate to inter- or intra-individual differences.

Differences in penguin comportment with respect to, e.g., stage of breeding cycle**, time of day** (e.g., Müller-Schwarze 1968), species, **colony location** (e.g., Cobley & Shears 1999), or **location of nest site** (e.g., Tenaza 1971), and **current activity** (commuting vs. incubating, e.g., Wilson, R.P. & al. 1991) have been described in various publications. Holmes & al. (2005), for instance, found **moulting** Royal penguins, *Eudyptes schlegeli*, to be substantially longer affected by human visitation than **incubating** penguins of the same species: While both groups responded at the greatest distances to a standard pedestrian stimulus, the behaviour of the latter was affected for up to 15 min after the visit occurred. Response differences (observed distance of first response, readiness to flee) related to **nest contents** (eggs, small or large chicks) have been stated for Adélie, *Pygoscelis adeliae* (e.g., Wilson, R.P. & al. 1991), African, *Spheniscus demersus* (Giese & al. unpubl. data), and Magellanic penguins, *S. magellanicus* (Cevasco & al. 2001). **Species** differences in vulnerability to human disturbance have been postulated by Ellenberg & al. (2006) with respect to Humboldt penguins, *S. humboldti*. Differences in comportment between entire colonies/ populations of the same species (here: Magellanic penguins, *S. magellanicus*) have been attributed to **habituation** (e.g. Walker & al. 2005, 2006; Cevasco & al. 2001), but a cautionary note has been convincingly put forward by Ellenberg & al. (2007), who state that in the majority of studies it has to date not been possible to determine whether observed 'unruffledness' in the face of human presence is due to habituation of individuals or rather related to the fact that afflicted penguins have left the area[43].

'Truly individual' differences (within groups studied at the same site and time, subjected to the same natural and/or experimental conditions) in **behaviour** have been noted or shown (figures/ tables) by several authors for Adélie, *Pygoscelis adeliae* (e.g. Giese 1998, Sladen 1958, Spurr 1974), and other penguins (e.g. Holmes 2007, for Gentoo, *P. papua*, Royal, *Eudyptes schlegeli*, and King, *Aptenodytes patagonicus*; Giese & al. unpubl. data, for African, *Spheniscus demersus*; Ellenberg & al. 2007, 2009, for Yellow-eyed, *Megadyptes antipodes*). While most publications present mean values ±SD or ±SE, these differences have sometimes resulted in a more fine-grained categorisation: Fowler (1999) assigned Magellanic penguins, *S. magellanicus*, to three response categories (neutral, alarm, aggression), and classifications according to three types of 'penguin personality/ character' (timid, calm, aggressive) have been used by, e.g., Ellenberg & al. (2007, 2009), for Yellow-eyed penguins.

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[43] For supporting evidence, also see Fowler (1999).

These distinctions come close to the **different coping strategies** proposed by animal welfare research: Wechsler (1995) distinguishes four coping strategies: 1. escape (increase distance to stimulus → flight behaviour), 2. remove (move stimulus away → aggressive behaviour), 3. search (for an absent stimulus → appetitive behaviour), and 4. wait (for a spontaneous change in the aversive stimulus → apathetic behaviour). While the third strategy does not apply to incubating penguins, the other three are clearly feasible and might to some extent help classify the different responses observed.

A number of publications have likewise mentioned or shown distinct[44] individual differences in (resting) **heart rate** for Adélie (e.g. Giese 1998, 1999, Culik & al. 1989, Culik 1992), and other penguins (e.g., DeVilliers & Giese 2004, DeVilliers & al. unpubl. data, for African, *Spheniscus demersus*; Ellenberg & al. 2006, for Humboldt, *S. humboldti*; Ellenberg & al. 2009, for Yellow-eyed, *Megadyptes antipodes*; Holmes & al. 2005, for Royal, *Eudyptes schlegeli*). Nimon (1997) found heart rate of undisturbed Gentoo penguins, *Pygoscelis papua* (n=8 penguins, 35 sessions, 15 s counting-intervals), to differ significantly between individuals, but not according to nest location (central vs. peripheral). Neither did she find significant day-to-day differences within individuals.

To encompass inter-individual differences in heart rate, publications on disturbance present mean heart rate changes in bpm (± SD, e.g., Giese 1998), bpm-values above resting heart rate (±SE, e.g., Nimon 1997), or calculate mean elevations (±SE) as a function of individual resting heart rate (e.g., Holmes & al. 2005). Following Baldock & Sibley (1990), individuals serve as their own control, i.e., heart rate elevations are compared against (resting) heart rate prior to visitation (all studies quoted and this study).

While the majority of disturbance studies examined both behaviour and heart rate, publications do not dwell on **interconnectedness of these parameters**. This study found at best a low correlation (s.a.) between vigilance and heart rate responses, which might either indicate individual response ‘preferences’ (either heart rate or behaviour, e.g. Duncan & Filshie 1979) or suggest **differential stimulus traits** – e.g., valence acquired by degree of novelty or difference in intensity – to predominantly elicit responses in certain parameters (e.g., heart rate upon becoming aware of stimulus, followed by vigilance; agonistic behaviour at very close range). As it is, a combination of the above said is proposed to have resulted in the substantial range of responses obtained from individual focal penguins examined in this study.

An intriguing further suggestion derives from the fact that in this study, correlations were calculated for all sessions pooled per FA (‘visited’ as well as ‘baseline’). As heart rate responses were commonly found in conjunction with vigilance during human, but not conspecific disturbance (see section 6.2.5), the overall low correlation might be due to different **response ‘preferences’ to different types of disturbance** stimuli.

Despite Nimon’s (1997, no significant day-to-day variation) findings, **within-day variation in responsiveness** appears to be another aspect worth examining, as birds subjected to considerable conspecific pestering or predatory action prior to visitation might be inclined to respond differently than they would, had visitation occurred after a prolonged period of quiet in the colony. This explanation was not tested directly (as pre-visit records only captured a maximum of 20 min[45] prior to visitor exposure); indirect evidence, however, is suggested to come from heightened response observed in the post-visit period, which might well have resulted in a stronger response

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[44] not always reported to be statistically significant

[45] truncated to 10 min after the completion of primary transcriptions, i.e., prior to analyses

level, had a further visit been effected. The suggestion is supported by observations on heart rate responses in African penguins (DeVilliers & al. unpubl. data), which were more pronounced during second than during first visitor approaches (time in-between visits: 1 hour). Conversely, Nimon (1997), reported within-season habituation to visits by tourist groups for the Gentoo penguins examined in her study, but these visits did not occur on the same day.

Visual appraisal provided further evidence for individuality in response to human visitation. While decreases in resting and increases in vigilance behaviour were found in most sessions both during- and post-visit, examination of **anti- and, particularly, syndirectional changes** additionally revealed other behaviours to be clearly influenced by visitation, even though these were exhibited in fewer sessions.

Differences, however, were not necessarily limited to **inter-individuality**, but were also observed within a given individual on different days, i.e., **intra-individually**. Thus, while in some sessions resting behaviour was exclusively replaced by increased vigilance (e.g., B33-2, 16.11.2000 morning visit = mv), the same bird would sometimes exhibit a mixed response consisting of vigilance, headshakes, and agonistic behaviours (e.g., B33-2, 17.11.2000 afternoon visit = av), vigilance, breeding, and headshakes (e.g., B33-2, 24.11.2000 mv) or vigilance, breeding, and agonistic behaviours (e.g., B33-2, 26.11.2000 av). The same is true with respect to different penguins visited on the same day (e.g., B3-2: almost exclusively vigilance; B4-1: vigilance, headshakes, agonistic behaviours; both 20.11.2000 mv) so that climatic influences appear unlikely to constitute an exclusive (in the sense of satisfactory on their own) explanation for intra-individual behaviour.

Differential expression of agonistic behaviour among individuals has already been discussed (see section 6.2.1), and attention has been drawn to the fact that to some extent expression of behaviour during visitation appeared to depend on behaviours expressed before the visit commenced. For generally rarely observed behaviours (e.g., longer bouts of preening or egg manipulation), the study did not yield a large enough dataset to establish whether this dependence was individual- or behaviour-specific, with the latter pointing towards the phenomenon of **emergent dynamics** rather than to inter-individual differences, i.e. response behaviour is **modulated by behaviour exhibited pre-stimulus presentation**. This observation is also supported by Boissy (1995, p. 169), who states that “[i]ntermediate degrees of fear usually lead to a conflict between the expression of fear and the activity in which the individual is engaged”. The outcome of this conflict depends on ‘degree of intermediacy’ of fear as well as on the strength of motivation with which the current activity is pursued.

Patterns of ranked responses during- and to some extent post-visitation were at times found to reflect a **persistently high or low level of response** (i.e. lowest level of expressed behaviour prior to visitation corresponding to lowest change level during/ post visitation) for FAs pooled by regime. This level, however, did not tally with hypothesised differences in severity of visiting regimes (regime differences are discussed in detail in section 6.2.6) but seemed likely to be due to differences among the penguins themselves rather than the regimes. These differences might but need not necessarily be **individual-specific**; other feasible explanations relate to micro-site (nest location within colony), comprising factors like differential **inter-nest distances**, and **conspecific** or **predatory pressure**. According to Ainley (2002), nests on the periphery are generally occupied by young and thus rather inexperienced breeders; even if these were exclusively found in first- but not second-row nests, however, the differences observed are unlikely to be related to ‘nest-distance from edge’, as first- and second-row nests were evenly distributed among the groups examined.

Inter-individual differences, on the other hand, might certainly be to some extent attributed to differential **age and/or breeding-experience**.

Examination of individual sessions likewise suggested responses during visitation to be partly **dependent on behavioural repertoire exhibited prior to visitation** (e.g., for breeding and comfort: higher proportions pre-visit more likely to be reduced during-visit; for agonistic behaviour: higher proportions pre-visit more likely to further increase during-visit).

With respect to occurrence of headshakes (also see topography charts in appendix 5.3.1-1), data analysed in THIS STUDY indicated a combination of site- (group location within colony), individual-, and situation-specificity, with headshakes being encountered more frequently in FAs-C than, e.g., in FAs-B, more often in FA-C2-2 than in other FAs from this group, and more often during and/or after than prior to visitation.

Moreover, it could be shown that for each behavioural parameter as well as for posture, the majority of post-visit responses either constituted an incomplete return to (IR; behaviour/ posture still altered in the same direction as during visitation, only less so, e.g. strong increase during, lesser increase post), or an 'overshooting' of pre-visit levels (O; behaviour/ posture altered antidirectionally to during-visitation, and more pronounced than pre-visit), but rarely represented a 'true' recovery. The magnitude of differences in response between pre- and post-visit found in individual sessions was extremely variable, and the range of between-period values (span from min. to max.) was substantial for all parameters. These findings are also suggested to be linked to individual differences which, again, are not necessarily restricted to inter-individuality, but equally likely to reflect a variation in intra-individual responsiveness resulting from **current 'state of being'**.

Therefore, temporal differences in rising (pre- to during-visit), waning (during- to post-visit), and persistence (post- vs. pre-visit) of responses found in different parameters appear to be additionally influenced by and to be thus partially related to different animal-mediated response 'preferences'.

Last, but not least, responses exhibited by currently not incubating conspecifics during and after human visitation (e.g. none, halt, move away, move into the colony) did not show a general trend, and there was no consistent linear relationship between human visitation and conspecific presence for any of the groups/ datasets examined (also see section 6.1.6.2). A more detailed analysis of 'group behaviour' would almost certainly reveal some patterns relating to, e.g., distance of visitor at first notice (e.g., BLUMSTEIN 2003), angle of visitor (e.g., MARTIN & al. 2004), relative position of penguins (close to or further away from own territory). Additionally, 'group behaviour' might be influenced by individuals, as VANHEEZIK & SEDDON (1990, p. 92) suggested with respect to beach groups of African penguins, *Spheniscus demersus*:

> "The flight reaction in penguins may be socially facilitated, its initiation depending on one timorous individual in the group acting as a trigger. Larger groups would be more likely to contain timorous individuals, and will therefore respond more readily to approach."

6.2.4.3 The Importance of Individuality

The **majority of individual-based penguin studies** to date focus on mean values across all focal birds examined; individual differences are often mentioned but rarely elucidated further (but see ELLENBERG & al. 2009; also DEVILLIERS & al. unpubl. data). This search for general results continues to be encouraged by publishers and scientific community alike, even though there seem to be cyclical re-appearances of advocating individual variation as a worthy field of knowledge (e.g., Bennett 1987; Williams 2008, Ellenberg & al. 2009, and references therein).

Turning for a moment to **laboratory studies** – i.e., experiments undertaken in the purportedly most controllable of environments – Richter & al. (2009, 2010) recently showed that a high degree of standardisation (e.g. with respect to age, sex, body weight, husbandry, and test procedures) did not result in lab-to-lab reproducibility of findings, whereas improved reproducibility of experimental results across laboratories was effected by systematic variation of experimental conditions (heterogenisation). It would thus seem that individuality remains of substantial influence even after non-natural (i.e., human) selection has striven to extinguish it (in laboratory animals), and consequently much more so in field conditions.

Interestingly, **early studies on penguins** did not leave the reader in any doubt concerning the individuality of the subjects described (e.g., publications by Bagshawe 1938; Levick 1914; Richdale 1945, 1949, 1951, 1957; Sladen 1958), even though some of them might occasionally have erred on the other side (particularly Levick's suppositions have at times proved untenable, cf. guardians for crèches). Sladen (1958, p. 37) detected individual differences in aggressiveness in Adélie penguins and ascribed them to a combination of temperament, sex, phase of breeding season and state of nourishment (also see section 6.2.1.3). He, as well as Penney (1968) recognised inter-individual differences in Adélie penguin response to humans (degrees of shyness/ boldness), and the latter additionally reported 'learned aversion' in banded birds, stating that he "generally found that banded birds reacted more strongly to my presence than unbanded ones did" (ibid., p. 90). Concerning Adélie penguin behaviour during nest-building, Sladen (1958, p. 42) observed great variation in the response of the bird occupying the site. He commented that "[s]uch sudden changes cannot be explained solely in terms of gonad development and/or 'releasers of behaviour mechanisms'. The whole psychological background of the two birds has to be considered, as well as external factors such as weather, degree of disturbance in neighbouring nests, or the possible effect of a human observer […]."

In particular with respect to adaptational capacities (and thus in this context, ability to habituate to and thus cope with human presence/ visitation), **inter-individual** differences seem of paramount importance, as "[a]daptive responses to environmental challenges are affected by preexisting [sic] characteristics of reactivity that are based on interactions between an individual's *genetic background* and *past environmental influences* on developmental and learning processes" (Boissy 1995, p. 178, italics in publication). These inter-individual differences have been examined and found in a number of vertebrate and invertebrate species (for the latter: octopi) (see, e.g., reviews by Koolhaas & al. 1999 on different coping styles, Wechsler 1995 on different coping strategies).

This study additionally draws attention to another level of individuality, viz., **intra-individual** differences. It is suggested that these need to be better understood before generalisations as to indicative behaviours (see below, Aim VI) and/or threshold distances (see below, Aim VII) can be made, even if such 'generalisations' be already modified by taking into account site- or species-specificity. The birds examined in this study showed intra-individual variations in response to visitation which were more likely attributable to 'general state of being' (depending on, e.g., predominant behaviour performed and/or differential subjection to of predatorial or conspecific disturbance stimuli prior to visitation) than to changes in the visiting stimulus on different days. Unless recognised, these variations might obscure the true impact of human disturbance.

6.2.5 Aim IV: Impact of Conspecific Disturbance vs. Human Visitation

H_0: There will be no differences in penguin responses to conspecific and human disturbance.

- H_1: Penguins will respond differently to conspecific than to human disturbance.

Recapitulation: All **visiting regimes** followed the **same time schedule**. The visitor(s) started to walk towards the penguin group at a distance of 20-25 m[46] from the colony edge. At pre-set distances (15 m, 5 m, and 3 m, respectively), the visitor(s) stayed for approx. 2 min before moving on to the next stop (from 15 m to 5 m, from 5 m to 3 m), resp. retreating (from 3 m back to base). Retreat to the initial distance (20-25 m) occurred in a straight line at the same pace as the approach and without any in-between stops.

In contrast, the extent and intensity of **conspecific presence and action** had not been manipulated.

In THIS STUDY, conspecific presence and action varied greatly between the groups/ datasets/ FAs, in both average and range. Responses to conspecifics were examined **before** and **after** human visitation (Chpts. 5.1, 5.2, and 5.3.1). With respect to focal groups (5.1), partial rank correlations additionally permitted direct comparison of impact of disturbance types (conspecific presence vs. human visitation) **during** visitation (s.b.).

6.2.5.1 Conclusions – Conspecific vs. Human Disturbance

With respect to absence of response differences towards conspecifics and humans, H_0 was successfully refuted.

Impact of **human** visitation was found to generally **exceed** that of **conspecific** presence and/or action as regards intensity of response and affected comportment parameters. The fact that several parameters were observed to change during human visitation – but not during conspecific disturbance – indicated a more profound disruption of penguin comportment by the former disturbance type. During human visitation, a number of penguins displayed a **gradation of behaviours** similar to that commonly found in response to conspecifics (decreased resting and increased vigilance at a greater distance, increased agonistic behaviour close up), with response changes occurring at substantially greater distances for humans than for conspecifics; but agonistic behaviours towards humans were not as ubiquitous as during interactions with conspecifics moving close to the focal animals' nests. A consistent response in heart rate was exclusively observed during human visitation, but not during conspecific encounters.

It is suggested that due to (Antarctic) penguin evolutionary history, changes in intensity (assessed, qualitatively)/ magnitude (measured, quantitatively) of behaviours displayed, rather than 'novel' behaviours should be expected when birds are subjected to a different and/or 'evolutionarily novel' type of disturbance stimulus (humans as predation-free predators).

In this context, a farther-reaching disturbance response (i.e., changes in behaviours unaffected by 'natural disturbers', viz., conspecific competitors) might indicate that display of evolved anti-

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[46] Maximum distance depended upon geography, i.e. the visitor(s) followed the foot line of the hill opposite the colony until they could approach the focal group in a straight line (see chapter 3, fig. 3-25).

competitor behaviour is experienced as ‘insufficient’ with respect to coping. Additionally, changes in structure and overall composition of comportment are proposed as a challenging but worthwhile field of investigation when examining differences between conspecific and human disturbance.

Following, results pertaining to quality and quantity of responses towards conspecifics are discussed in detail and subsequently compared to responses exhibited towards human visitation.

6.2.5.2 Placing Results Obtained into Context

Responses to conspecifics were **examined empirically**, i.e., upon occurrence, a ‘common practice’ found in most studies primarily concerned with human disturbance (s.b.). This procedure appears well defendable, given the fact that detailed descriptions of penguin behaviour towards conspecifics have been compiled in reports on general breeding biology.

Descriptions of, e.g., territorial disputes[47] involving – often graded – agonistic behaviours are found in all studies on penguin biology (e.g., Ainley 2002; Ainley & al. 1983; Boersma 1977; Eggleton & Siegfried 1979; Penney 1968; Roberts 1940; Seddon 1991; Sladen 1958, van Zinderen Bakker 1971; Warham 1963, 1971, 1972, 1974a, b). As regards burrow- and cave-dwelling Little blue penguins, *Eudyptula minor*, response repertoire and intensity has been shown to vary according to habitat (e.g., Waas 1990). Responses towards conspecifics including aggression towards chicks[48] (DeLéon & al. 2002) and agonistic responses to attempted or effected stone theft (Moreno & al. 1995a, b) have been reported for Chinstrap penguins, *Pygoscelis antarctica*.

For studies on human disturbance, inclusion of extent of response to conspecifics (and often predators as well) serves as a **comparative basis** for gauging impact of human disturbance as experienced by the birds examined. Responses to conspecifics found in these studies are therefore discussed, before turning to the comparative aspect.

6.2.5.2.1 Responses to Conspecifics

Focal-group evaluations found that response to conspecific **presence** (for discussion of utility of parameter, see section 6.1.6.1) did not tally with either absolute or proportional (‘relativised’ by size of focal group) numbers of conspecifics observed, as higher numbers of conspecifics present (e.g., group C) did not generally result in higher r^2-values for any of the parameters examined (focal-group behaviour, posture). Nevertheless, they suggested **directions** of response to be consistent as regards vigilance (increase) and resting behaviour (decrease).

Additionally, focal-animal visual appraisal indicated a **graded response** towards conspecific **action** (movement in three distances from and certain behaviours performed directly at the focal nest) for some of the comportment parameters examined: Increased vigilance (15 of 51 sessions) and scattering (6 of 49 sessions) as well as decreased rest (9 of 51 sessions) were observed during conspecific **movement irrespective of distance** to the focal nest, and increased agonistic behaviour (19 of 40 sessions) was displayed towards **conspecific movement at the focal nest**. Visual appraisal did not find consistent heart rate responses to conspecifics, and correlations obtained for individual focal animals likewise indicated conspecific action to influence vigilance and agonistic behaviours, but not heart rate. Given that responses had to exhibit within-session consistency (i.e., responses in only half the encounters observed were not considered), findings from THIS

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[47] being a very common interaction between currently incubating and currently non-incubating penguins

[48] Le Bohec & al. (2005, King penguins, *Aptenodytes patagonicus*) as well as Seddon & van Heezik (1993, African penguins, *Spheniscus demersus*) have considered aggression towards chicks a major factor for the development of crèches.

STUDY are not directly comparable to those based on division of positive responses by total encounters observed (e.g., NIMON 1997, s.b.).

Same as THIS STUDY[49] (focal-animal evaluations), NIMON (1997) examined conspecific intrusion in three different zones of increasing distance from the focal nest for Gentoo penguins, *Pygoscelis papua*. She found that 48 % of 781 conspecific actions recorded elicited an observable behavioural reaction, with all responses involving either 'high threat[50]' (mainly zone-1, rarely zone-2, never zone-3) or 'alert' (mainly zones-1 and -2, occasionally zone-3), but not 'low threat[51]'. Concerning heart rate responses, she reported zone-1, but not zone-2 or zone-3 intrusion by conspecifics to exert a significant effect (increase) on penguin heart rate with a mean overall increase (all penguins, n=35 sessions from 8 penguins) of 8.7 bpm (SE: 1.0), and ranges in mean increase (per penguin) from 3.7 bpm (SE: 1.1) to 19.2 bpm (SE: 5.1). For Royal penguins, *Eudyptes schlegeli*, HOLMES & al. (2005) reported primarily increased agonistic behaviour (vigilance is shown to be exhibited but not specified to be elevated as compared to undisturbed penguins) and heart rate elevated above resting values in response to conspecifics walking past the nest. ELLENBERG & al. (2006) found returning partners to elicit the strongest heart rate response to natural stimuli in Humboldt penguins, *Spheniscus humboldti* (164 % RHR), but elevations were extremely transient, usually returning to RHR range within seconds.

Results obtained in THIS STUDY suggest **general conspecific movement** (further away from nest) to be perceived as less threatening to penguins – thereby drawing a vigilance response (with vigilance behaviour 'replacing' resting behaviour, cf. visual appraisal), whereas **movement close to the focal nest** incurs the risk of nest stone theft or direct aggression, and draws a more forceful response, i.e., agonistic behaviour. Since agonistic behaviours rarely take up longer stretches of time, 'replacement' of resting behaviour does not necessarily become apparent.

As an aside: In a similar manner, skua low overflights (further away) cause a stronger response in vigilance behaviour, while during skua presence on ground (closer) agonistic responses are added.

6.2.5.2.2 Responses to Conspecifics vs. Responses to Human Visitation

With respect to focal groups, THIS STUDY found **conspecific presence during human visitation** to exert an influence on resting ('rest&Co') and vigilance ('alert') responses only in the datasets subjected to the least severe visiting regime (1 P, S&S: B_2, C_1), whereas human visitation itself more strongly affected these parameters in the remaining groups. In general, there was **little evidence of a complementary relationship** of the two types of disturbances, with only three cases in which weak responses to human visitation were complemented by pronounced responses to conspecific presence. All these had been subjected to the regime 1 P, S&S (i.e., 'alert': C_1; 'rest&Co': B_2, C_1). On the level of focal-group evaluations, findings thus suggested **conspecific** presence to constitute a **'background noise'** on top of which **human visitation** exerted an **additional impact** which clearly exceeded that of conspecifics in all but the 'mildest' of visiting regimes.

Reports on conspecific impact during human visitation were not found in published studies, but NIMON (1997, p. 118) found "no correlation between tendency to experience a heart rate reaction

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[49] The idea of identifying concentric nest zones was adopted from NIMON.

[50] NIMON (1997, p. 53): "High Threat includes all the aggressive or fighting behaviour of gentoo penguins remaining prone on the nest, including pecking, attacking or grasping the intruder with the beak. It also includes threat postures such as pecking (and missing) or opening and closing the beak while shaking the head."

[51] NIMON (1997, p. 52f): "Low Threat: (ritualised threat display) incubating penguin raises its head and neck, points closed bill upwards; it may also wave the head in a circular motion, while keeping bill outstretched and closed."

during the approach of a large visitor group and the same tendency during zone 1 [directly at the FA's nest site] interaction with a penguin intruder", strongly suggesting **differential perception/ weighting of stimuli** for her subjects.

Focal-animal evaluations (behaviour elements) indicated vigilance behaviour to be more closely related to extent of human than conspecific disturbance for most, but not all focal birds examined, whereas agonistic behaviour correlated more strongly with conspecific than human disturbance. Moreover, agonistic behaviour towards conspecifics was shown by all focal birds, while only half of them exhibited this response during human disturbance.

For Gentoo penguins Nimon (1997) observed threat behaviours towards conspecifics ('high threat'), but not towards humans, while Holmes & al. (2007/ 2008) report increased agonistic behaviours during human visitation (but do not indicate whether levels were higher than those observed towards conspecifics).

Visual appraisal of overall comportment found that only the parameters vigilance, scattering, agonistic (all increase) and resting behaviour (decrease) could be considered sensitive to changes in conspecific action; in contrast, all parameters examined changed during human visitation. The **gradation of vigilance and agonistic responses** (vigilance exhibited further away, agonistics closer up) found during human visitation, however, appeared to be similar to that found during conspecific disturbance, albeit at fundamentally different distances: Agonistic behaviour including the offensive elements 'point' and 'gape' was displayed at a distance of 3 m for humans; with regard to conspecifics, particularly these offensive elements were most commonly seen to occur in response to conspecific action immediately at the focal penguins' nests.

The fact that reaction patterns (i.e., graded response) of behaviours commonly used in response to conspecifics (and predators) were transferred to humans, while behaviours outside this response repertoire were additionally affected (s.a., all comportment parameters analysed), is suggested to indicate a substantially **greater impact of human vs. conspecific disturbance**[52]. The 'overhang' of impact of humans as compared to conspecifics is also seen in the persisting alterations found during the post-visit period in this and other studies discussed in the previous sections (see Aim I and Aim II).

Most published studies agree that heart rate responses to human visitation were more pronounced and/or longer lasting than those exhibited towards conspecifics. Giese (1998), for instance, found heart rate responses of Adélie penguins to conspecifics (no type of interaction specified) to be below those recorded for human approach to within 5 m of the penguin, and Ellenberg & al. (2006) reported higher heart rate increases and substantially longer recovery times for Humboldt penguins, *Spheniscus humboldti*, subjected to human visitation as compared to conspecific interaction.

This study did not encounter consistent heart rate responses to conspecific presence action at all, whereas heart rate responses to human visitation were widespread and distinct (see Aim II).

6.2.5.3 Lack of Human-Specific Comportment

It is suggested that in terms of Antarctic penguin behavioural evolution – which has for the greatest part taken place in the absence of humans, and, perhaps equally important, terrestrial predators; e.g. Simpson 1976) – Antarctic penguins should not be expected to exhibit **'human-specific'**

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[52] With respect to skuas, qualitative observations indicated them to exceed a greater 'point-impact' (cf. stimulus trait intensity, in this case, velocity of appearance as well as distance from focal nest) on penguins than did human visitation. Greater 'point-impact' was, however, complemented by a quicker recovery after stimulus removal.

behaviours in the face of disturbance by visitation. Penguin behaviour has, however, evolved alongside conspecific competitors (, e.g., nest stone theft, nest appropriation) and aerial predators (nest attack, egg or chick theft), with the latter at times approaching them on the ground.

The search for indicative behaviours (see Aim VI) would thus seem primarily limited to **differential intensities** (qualitatively: e.g. heightened vigilance towards humans as compared to conspecifics)/ **magnitudes** (quantitatively: e.g., twice as much vigilance towards humans as compared to conspecifics) in the behaviours displayed towards human vs. natural ‘intruders’, as proposed in the concept of **humans as predation-free predators** (e.g., PÉPIN & al. 1996, BEALE & MONAGHAN 2004a). In the absence of humans, these behaviours are also observed, and might even reach equally high proportions, particularly during predator disturbance.

For such behaviours, it is important to keep in mind that **humans** will always come ‘on top of everything else’, and must therefore be seen **as an additional rather than an alternative source of disturbance**.

Moreover, the **extent of disturbance response** in terms of comportment parameters affected should be examined, as this might indicate the degree to which display of evolved anti-competitor behaviour is experienced as ‘insufficient’ with respect to coping.

Last, but not least, deviations from naturally evolved behaviour are quite feasible on the level of **‘syntax’** (overall structure: generally shorter/ longer phases; within-parameter structure: shorter phases of ‘rest’ and longer phases of ‘vigilance’) as well as **composition** of behaviour (distribution of phases of different behaviour systems in terms of number and duration) so that identification and quantification of changes in behavioural topography (conspecific disturbance vs. human visitation) would appear particularly worthwhile – if challenging, and time-consuming. THIS STUDY has presented evidence for both ‘types’ of response (see Aim I and Aim II).

6.2.6 Aim V: Impact of Different Visiting Regimes (Visitor Conduct and Number)

H_0: There will be no differences in penguin responses to different visiting regimes.

- H_{1A}: Penguins will react more strongly/ less weakly to ‘loud and fast’ as compared to ‘silent and slow’ visitor(s).
- H_{1B}: Penguins will react more strongly/ less weakly to 3 visitors as compared to 1 visitor.

Recapitulation: In terms of severity, loud and fast visitation (L&F) is hypothesised to exceed impact of silent and slow visitation (S&S), while 3 visitors (3 P) are assumed to exert a greater impact than 1 visitor (1 P). Ranking the regimes employed in THIS STUDY, the following order would ensue:

3 P, L&F (FAs-Y) > 1 P, L&F (FAs-B_1; C_2) $\geq$ 3 P, S&S (FAs-X) > 1 P, S&S (FAs-C_1; B_2)

N.b.: Concerning **focal-animal** analyses, all sessions from FAs-B_2 were discarded due to insufficient visibility of FAs. Three sessions from the first day post-switch were available for FAs-C_2. FAs-$C_{1,2}$ will be summarily referred to as having been subjected to ‘predominantly the regime 1 P, S&S’, as next to no difference in comportment (as compared to pre-switch) had been observed in these sessions.

6.2.6.1 Conclusions – Impact of Different Visiting Regimes

With respect to absence of response differences towards different visiting regimes, H_0 was successfully refuted. Differences in (very disparate) visitor conduct (H_{1A}), however, elicited more obvious response differences than (small) differences in visitor number (H_{1B}) so that the entire gradation of regimes (see recapitulation) was not consistently 'confirmed'.

THIS STUDY found that the **regime differences** hypothesised were **detectable on all levels** (How many? → consistency; How much? → magnitude of changes in prevalence; In what way? → 'syntax', composition) of focal-animal comportment examined, but discriminatory capacity varied between the levels. On all levels, the greatest unanimity in most pronounced responses was observed for FAs subjected to the regime hypothesised to exert the greatest impact (3 P, L&F), while least pronounced responses were most frequently found for FAs visited in the least severe manner (1 P, S&S). The entire gradation order, however, was not consistently detected.

Capacity to distinguish between regimes appeared to be at least partially dependent on sampling method (ISS every 30 s vs. second-by-second transcription, see section 6.1.3.1). Differences may also relate to individuals sampled (rows 1 to 4 for focal groups vs. rows 1 and 2 for focal animals), but 'coarser' measures (single key values, i.e. period-means, DiM, MoD) employed in analyses of focal-animal data were similarly restricted, indicating that post-transcription methods of averaging results were likewise prone to result in losses in discriminatory capacity.

FA-dependent rather than regime-mediated response **'preferences'** (comportment parameter), response **intensities** (quantitatively measured as differential magnitudes of response to 'same' stimulus), and response **propensities** (readiness to respond/ cease responding/ continue to respond), are suggested to merit further investigation, as these need to be incorporated in future models of response, if overall results are proposed to adequately reflect focal-animal 'reality'.

With respect to responses of incubating birds to disturbance, their **perception of disturbance** (animal's point of view) is assumed to be of greater relevance than the **purpose** (tourism, leisure, science) **assigned** to it by the disturber themselves (disturber's point of view). Cross-testing visitor conduct (loud and fast vs. silent and slow) and number (3 vs. 1) in THIS STUDY generally suggested a greater influence of conduct than number, but did not permit extrapolation with respect to larger groups.

The observation that **moving stimuli** generally elicited a stronger heart rate response than still ones (see Aim II) irrespective of direction (crouching down vs. getting up, retreat vs. approach), sheds doubt on the idea of a closer approach being less disturbing if the visitor keeps low (some tour guides, pers. obs.). This might be an advisable behaviour if close approach cannot be avoided (as in the case of, e.g., artificial egg deployment or nest checks during monitoring), and posture is continuously kept low. Given the fact, however, that crouching as well as getting up, approach as well as retreat was found to cause heart rate to peak and behaviour responses to increase, this procedure should not be favoured over remaining at a larger distance in the first place.

Apart from visitor conduct (e.g., noise level, speed, and abruptness of movements) and number, **penguin responses** are suggested to be additionally **influenced** by factors such as duration of exposure or tightness of visiting group, all of which will interact with stimulus perception. Furthermore, individual perception is likely to be mediated to an as yet unquantified extent by the stimulus traits outlined in section 6.2.2 and 6.2.3 (i.e., valence acquired over the course of evolutionary history; valence acquired through increased intensity or degree of novelty of stimulus; valence acquired by individual or social learning).

The fact that animal-dependent patterns were more often found with respect to total phase number, while graded differences in impact of visiting regime were more readily discernible for changes in **total phase time** indicates that the latter ought to be considered **superior in terms of gauging impact of human visitation**. The confounding factor of animal-mediated responses (s.a.) is suggested to deserve closer investigation in this context as well.

The **stimulus of human visitation is multi-facetted** and its variability increases with number of people present; true habituation of penguins to anything but ‘strictly choreographed’ human contact therefore seems unlikely. Selective utilisation of areas differently frequented by humans (with more ‘timid’ penguins leaving areas in which they are subjected to frequent human contact), in contrast, appears a more probable explanation in a number of cases of reported ‘habituation’, and consequences should be taken into account when deciding on visitor regulation.

Following, results pertaining to the question of influence of visitor conduct and number on responses of penguins subjected to human visitation will be discussed in detail.

For want of better placement and because of their undisputed high degree of disturbance, literature reports on invasive ‘hands-on activities’ as capture or stomach flushing are discussed within the section on visitor conduct. Conduct likewise includes different postures adopted by humans during visitation, i.e. standing vs. kneeling/ crouching. As most studies investigated *either* penguin responses to different visitor conducts *or* to different visitor numbers, these are initially examined separately; following, results on cross-tests are briefly compared. Subsequently, relevance of findings with respect to impact of tourism and scientific research is pointed out, and evidence as to the penguins’ habituation potential to human visitation is considered.

6.2.6.2 Placing Results Obtained into Context

6.2.6.2.1 Influence of Visitor Conduct

On the focal-group level and within the behaviour categories ‘alert’ and ‘rest&Co’, THIS STUDY found that responses to different visiting regimes **separated the silent and slow regimes from the loud and fast ones** for groups X and Y (3 visitors), as well as for first datasets at groups B and C (initial 1 visitor regimes): Silent and slow visitation (S&S: groups X and C_1) elicited less of a response for 1 visitor as well as 3 visitors than loud and fast visitation (L&F: groups Y and B_1).

For group B, the same was true with respect to first and second datasets (B_1, 1 P, L&F; B_2, 1 P, S&S), as stronger responses were found to loud and fast visitation (B_1) than to silent and slow visitation (B_2). For group C, responses in the category ‘rest&Co’ likewise reflected this trend; but there was little distinction between regimes as regards the category ‘alert’, and slightly stronger responses were found in the first dataset (silent and slow visitation) than in the second (loud and fast visitation). As mentioned above, both second datasets suffered from the confounding variable ‘chick hatching’, an interpretation in terms of habituation thus lacks a viable basis, and has consequently not been ventured.

Focal-animal evaluations in THIS STUDY likewise indicated a generally greater impact for loud and fast than for silent and slow visitor conduct with respect to both behaviour and heart rate (s.b.) responses.

Concerning Gentoo penguin (*Pygoscelis papua*) behaviour, NIMON (1997, p. 104) found “no unusual or notable behavioural response to the approach or period of observation” during **gradual approaches by a single well-behaved visitor** to within 3 m. In contrast, penguins subjected to a **single visitor’s brisk approach** to within 1 m (note change in minimum distance in addition to change in conduct) of the nest were "primarily Alert throughout the period of exposure to the visitor, and did not relax into an At Rest posture [sic]" (ibid., p. 105).

As for further literature on differential human conduct, studies published later than Nimon (1997) did not subject penguins to 'careless' visitors (i.e., nothing equating loud and fast visitation in this study or Nimon's brisk approach). Instead, differences in 'conduct' reported pertain to **'human postures'** (standing vs. crouching/ kneeling, getting up).

Giese (1998) reports changes in Adélie penguin (*P. adeliae*) response to kneeling vs. standing of a single visitor only with respect to heart rate (s.b.). Holmes & al. (2005, p. 343) found both heart rate (s.b.) and vigilance behaviour to increase in Royal penguins (*Eudyptes schlegeli*) when the visitor moved into a crouching position and "when the pedestrian stood to leave", with decreases in both parameters observed while the visitor kept low.

Heart rate responses of focal animals subjected to loud and fast visitation in this study showed great inter- and intra-individual differences, but the highest maximum values were measured during **loud and fast visitation** (e.g., B4-1: from max. 43 beats per 20 s pre-visit to max. 71 beats per 20 s during-visit; Y5-1: from max. 33 beats per 20 s pre-visit to max. 57 beats per 20 s during-visit). As regards differences with respect to total phase time, visitor conduct- rather than regime-mediated responses were found for the heart rate category 'above' (RHR ±2 SD) from pre- to during-visitation, and for categories 'within' and 'above' from pre- to post-visitation. Moreover, this study found overall propensity to continue to respond beyond the withdrawal of disturbance stimulus (comparing magnitudes of changes in total phase time for all comportment parameters examined) to be primarily linked to visitor conduct, with lower values for **silent and slow** regimes than for **loud and fast** ones. An additional influence of visitor number (s.b.) was restricted to loud and fast regimes.

Adélie penguin (*Pygoscelis adeliae*) heart rate responses to approach were reported by various authors. Wilson, R.P. & al. (1991) and Culik & al. (1990a) found heart rate of breeding penguins to distinctly increase (from 76 bpm to 140 bpm and from 80 bpm to 127 bpm, resp.) when **approached** by a single **slowly** walking human. For a well-behaved visitor's approach to 5 m, heart rate increases of a similar magnitude were reported by Giese (1998). She additionally found **crouching** to elicit less of a response than **standing**, but subsequent **getting up** from that position to again cause increased elevations.

Heart rate elevations during human approach, however, were substantially lower than those obtained during **capture** (Wilson, R.P. & al. 1991; Culik & al. 1990a: increase to 287 bpm and 310 bpm, resp.) and **forced immobility** (160 bpm 1 min after the bird had been placed into a holding bag; Wilson, R.P. & al. 1991).

Nimon (1997) found no significant difference between overall pre- and during-visit heart rate in Gentoo penguins, *P. papua*, subjected to **gradual approach by a single well-behaved visitor** to within 3 m. She (ibid., p. 103f.) reported that upon the single visitor's reaching minimum approach distance, "heart rates sometimes showed a brief increase for spells of 10 or 20 seconds only. Maximum heart rates […] were on average 16.2 bpm higher (*se* = 3.7, *range* 1.6-47.9) than mean heart rate prior to human approach". In contrast, she found substantially more pronounced heart rate changes in penguins subjected to a **single visitor's brisk approach** to within 1 m of the nest (note change of minimum distance in addition to change in conduct), with lasting mean elevations of 50.5 bpm (SE: 17.7; visitor stand above nest) and 18.5 bpm (SE: 6.6; visitor crouch beside nest), respectively. No decrease was observed until the visitor left, and after this treatment, pre-visit levels were not reached again until several minutes after the visitor had been out of sight.

In naïve African penguins, *Spheniscus demersus* (DeVilliers & al. unpubl. data), **approaches by a single well-behaved human visitor** resulted in an average increase in heart rate of 41 % over pre-approach levels (mean: 117 bpm, SD: 21.0). The authors found significantly higher peak heart rates in response to the visitor's **standing** near nests than if the visitor **knelt**, but subsequent **getting up** caused heart rate to re-increase. Recovery time was highly individual, with the majority of birds recovering within a minute, and heart rates of four birds remaining substantially elevated even 10 min post-visit. The maximum heart rate response observed during human visitation (203 bpm) was approximately equal to the minimum response recorded during **stomach-flushing**[53] (199 bpm).

More pronounced responses to **capture** and **restraint** than to **visitation** were likewise obtained by Walker & al. (2006) for both behavioural and hormonal responses of male Magellanic penguins, *Spheniscus magellanicus*.

For Royal penguins, *Eudyptes schlegeli*, Holmes & al. (2005) reported significant inter-individual differences in resting heart rate and a mean increase of 23 % over resting heart rate during **approach by a single well-behaved visitor** to 5 m. According to their publication (ibid., p. 343), "[h]eart rate […] peaked when the pedestrian reached 5 m, at 1.7 times resting heart rate […]". Further peaks were recorded when the visitor **crouched** (downward movement), and **stood up again** (upward movement), but heart rate post-visit was not significantly different from pre-visit levels.

Ranking impact of conduct according to severity of behaviour and/or heart rate responses obtained, **invasive** procedures (capture, stomach-flushing) appear to be distinctly set off from **non-invasive** (approach, postural alterations) procedures, but results on African penguin heart rate (DeVilliers & al. unpubl. data) suggest that the gap is not quite as large as one might assume. As regards different conducts adopted during visitation, **loud and fast** or brisk visitation draws a more pronounced response than **silent and slow**/ well-behaved/ conscientious visitation. With respect to height levels, **standing** 'above' (looming over) the penguins is generally reported to result in more pronounced alterations of comportment than **crouching**/ kneeling 'beside' (more or less the same height level) them. The fact that vertical movement both into and out of that posture elicits considerable (re-)increases in response, however, suggests that impact of crouching should be evaluated in that context (as few people will approach, stay, and retreat in that posture).

6.2.6.2.2 Influence of Visitor Number

In this study, focal-group (but not focal-animal) evaluations indicated differences in response to **1 vs. 3 visitors** to be of relevance to expression of behaviours 'alert' and 'rest&Co' with respect to the silent and slow regimes only.

Literature reports are quite disparate as regards influence of visitor number. Holmes (2004, p. 58) reported that "the frequency and duration of vigilant activity was significantly greater in the **presence of groups of people** (5 visitors) than **single persons**, suggesting that Gentoo penguins, *Pygoscelis papua*, associated a higher level of perceived risk with increased numbers of people during pedestrian visitation". Nimon (1997), in contrast, found visitation of well-behaved **single visitors** as well as **small groups** (3-5 visitors) not to exert an influence on Gentoo penguin behaviour. Concerning (equally conscientious) **larger groups of 15 or more visitors**, the approach phase caused the strongest responses (65 % alert postures [sic], beginning when the group had approached to a 15-20 m distance), but behavioural response showed a marked reduction (49 %) when people had reached the 5 m distance and did not approach any closer.

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[53] e.g., for research on feeding ecology or prey availability

Far stronger responses than those found in Adélie or Gentoo penguins were obtained for African penguins, *Spheniscus demersus*, but as the two studies mentioned here were conducted at different locations, differences between these appear likely to have been (additionally) influenced by factors other than number of visitors: At Jutten Island, Hockey & Hallinan (1981) found nest-prospecting birds to be completely absent after a **single human**'s passing through a low-density colony on four consecutive days. Additionally, they reported (ibid., p. 60) incubating birds close to the transect line to have "sometimes left their eggs and these were depredated by kelp gulls, *Larus dominicanus*". At another location (Dassen Island) 56 % of all penguins examined exhibited agonistic activity during approach by **3 people on foot** (Giese & al., unpubl. data), 22 % showed no change in behaviour, a further 22 % shifted on nest, and 11 % temporarily vacated their nests (no predation observed). Additionally, an increase in alertness was reported.

Burger & Gochfeld (2007) found that **increases in numbers of tourists** in Emperor penguins', *Aptenodytes forsteri*, paths explained more than 50% of the variance and significantly increased distance of first notice (mean: 35.6 m), distance of change of direction (mean : 22.8 m), and number and duration of pauses. They observed behaviour of penguins to follow a dose-response, with increases in number of people tallying with increases in severity of penguin responses.

In this study, Adélie penguin, *Pygoscelis adeliae*, differences in heart rate increases were not observed to be consistent between 1 or 3 visitors. Rather than postulating 3 visitors not to exert an impact different from that of a single visitor, such extrapolations are considered unsound, given the small numerical difference (1 vs. 3) and the compactness of the 'visiting trio' (also see section 6.1.5).

Nimon's (1997, p. 116) findings with respect to heart rate responses to group visitation by **3-5 well-behaved people** indicated "no general tendency for penguin heart rate to increase according to the approach or presence of the visitor group". Concerning **large**, but equally **conscientious visitor groups** (above 15 and up to 50 people), she did not find a universal heart rate response, and if heart rate increased, it did so during approach to 5 m (mean increase: 11.7 bpm, SE: 4.0), and subsequently subsided to a mean increase of 5.7 bpm (SE: 1.8) as the group remained at 5 m.

Neither literature nor this study provides unanimous evidence to permit **ranking impact of visitor number** according to severity of behaviour and/or heart rate responses obtained. While moderately increased visitor numbers were found to elicit distinctly stronger responses in some studies (e.g., Holmes 2004; Gentoos; focal group analyses in this study), high visitor numbers appeared to be of little (e.g., Nimon 1997; Gentoos) or considerable additional consequence in others (Burger & Gochfeld 2007; Emperors).

6.2.6.2.3 Influence of Visitor Number and Conduct Combined

With respect to focal-group but not focal-animal evaluations, **differences between the two 3 visitor-regimes** (loud and fast: Y; silent and slow: X) were **less pronounced than those between the initial two 1 visitor-regimes** (loud and fast: B_1; silent and slow: C_1) AND their respective response values 'fell in behind' the regime 1 P, L&F (B_1). This resulted in conduct- (L&F regimes responding more strongly than S&S regimes) rather than regime-mediated responses (which postulated 3 P, L&F to elicit stronger responses than 1 P, L&F) obtained through focal-group analyses. As outlined in section 6.2.2, focal-animal, but not focal-group evaluations were able to capture continuation of responses (as opposed to disjunct point-responses, ISS), which is proposed to be partly responsible for differences in results obtained. An additional **'confounding factor'** (see section 6.1) is suggested to result from the compactness of the **visiting trio**, which might have rendered numerical differences less distinguishable to the penguins than envisaged by its creator during construction. In contrast, the fact that the clothing of the puppets responded to weather conditions (i.e., wind moving the folds) regardless of visiting regime and may thus have resulted in rather similar perception of the stimulus, is proposed to reflect climatic reality, and needs to be kept in mind when trying to gauge one's impact on penguins. Studies should strive to provide the number of visitors required as 'live visitors' and have usually done so, e.g., HOLMES 2004; GIESE & al. unpubl. data, NIMON 1997.

While the former two studies did not cross-test conduct and number, NIMON (1997) found influence of visitor conduct to considerably exceed influence of visitor number. She reported Gentoo penguins to remain 'alert' and to experience a continuous, high, and long-lasting increase in heart rate throughout a **'brisk-approach-visit' by a single person**, whereas **quiet visits by groups of 3-5** visitors (incl. 5 min at 5 m) did not change the penguins' average behaviour and produced only transient and distinctly lower heart rate elevations.

In THIS THESIS, more fine-grained analyses of focal-animal comportment, viz., behavioural topography, frequently found the visiting regime 3 P, L&F (FAs-Y) to elicit most pronounced responses. Despite the 'confounding factors' mentioned for focal groups (particularly compactness of visiting trio), addition of rank positions encountered at each visiting stage and each post-visit interval, revealed an overall greater number of **most pronounced responses for FAs-Y (3 P, L&F)**, complemented by an overall greater number of **least pronounced responses for FAs-C$_{1,2}$ (predominantly 1 P, S&S)**.

Separate examination of visit and post-visit periods completely supported hypothesised severity of regime with respect to rank positions most frequently occupied **during** visitation (in the order of FAs-Y ±4, FAs-B$_1$ ±3, FAs-X ±2, and FAs-C$_{1,2}$ ±1). **After** visitation, conduct- but not regime-mediated differences appeared to persist: Rank ±4 was most frequently occupied by FAs-B$_1$ (1 P, L&F), closely followed by FAs-Y. In the silent and slow regimes, order was likewise reversed with third ranks (±3) most frequently occupied by FAs-C$_{1,2}$, and FAs-X (3 P, S&S) most often exhibiting least pronounced responses (±1). In line with overall waning of responses, all FAs – except FAs-Y – were equally often encountered on rank ±2. In contrast, summed up rank positions for *DiM*- (differences in period medians) as well as *MoD-values* (median between-period differences) were only able to reliably distinguish between **most and least severe regimes** (as hypothesised: FAs-Y, 3 P, L&F vs. FAs-C$_{1,2}$, 1 P, S&S), which always retained highest sums of most (±4) pronounced ranks, and depicted highest sums for least (±1) pronounced ranks with a single exception (median of differences from during- to post-visitation), whereas neither key value exhibited sensitivity with respect to the middle ranks (±2, ±3).

With the evaluations at hand[54], it is impossible to decide without doubt whether the improved distinction between regimes effected by focal-animal evaluations is primarily due to the fact that the fewer penguin subjects observed as focal animals formed a distinct subgroup of those analysed as focal groups (e.g., due to being exclusively positioned in first or second rows), or indeed emphasises an increased chance of picking up changes when sampling points are less spaced out (s-by-s vs. 30 s), but the latter is suggested to be more likely. Furthermore, given the statistic property of median values (i.e., relative robustness towards deviations), results stress that it was primarily the regimes hypothesised to represent the most and least severe in terms of impact that elicited a certain **unity with respect to intensity** (and indeed magnitude) of response changes across comportment parameters.

THIS STUDY additionally examined regime differences in ***total phase number*** and ***time*** for selected categories, viz., 'rest', 'vigilance', 'interruptions s.l.', 'heart rate – within' (mean resting heart rate

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[54] The thought of a follow-up second-by-second examination of each focal-group subject was abandoned.

± 2 SD), and ‘heart rate – above’. Findings suggested a **complex interaction of regime/ conduct and individuality**, particularly with respect to response propensities (examined across all comportment parameters): Ranked magnitudes of response from pre- to during-visitation (overall propensity to respond) were regime-dependent with respect to total phase time; as for total phase number, conduct-dependence appeared likely (loud and fast visitation resulting in more pronounced changes than silent and slow). In contrast, changes from during- to post-visitation (overall propensity to cease to respond) observed in both total phase number and time appeared animal-mediated rather than related to hypothesised regime-differences. Additionally, differences in overall propensity to continue to respond beyond the withdrawal of disturbance stimulus (pre- vs. post-visitation) tallied with graded differences in impact of visiting regime with respect to total phase number, but seemed to be primarily linked to visitor conduct in terms of total phase time, with lower values for silent and slow regimes than for loud and fast ones. The additional distinction between visitor number (1 vs. 3) was apparent in the loud and fast regimes only.

These findings might suggest **‘selective decoupling’** upon cessation of disturbance stimuli, with a **longer-lasting impact for visitor conduct than visitor number**.

On the whole and considering results obtained in THIS and already published studies, an **attempt to unequivocally rank** visiting regimes according to the **combination of conduct and number** thus appears to be destined to a quick demise in a dead end. Evidence has been provided as to the fact that careless conduct substantially affects penguin responses (NIMON 1997 as well as THIS STUDY) and that increased numbers of disturbers result in increased responses (e.g., HOLMES 2004; BURGER & GOCHFELD 2007). It could also be shown that detailed analyses of changes in overall comportment revealed regime-graded responses that went undetected by less sensitive sampling methods and/or examination of isolated comportment parameters.

What remains to be investigated, however, is the extent to which controlling one aspect (e.g., conduct) might alleviate perceived severity of the other (i.e. number). Until a more conclusive body of evidence exists, ‘the less the better’ appears to be the only well-substantiated advice to offer with respect to both aspects.

6.2.6.3 Tourism vs. Scientific Research

Trying to integrate the above-said into the context of touristic vs. scientific disturbance, the **perception of disturbance** (animal’s point of view) may safely be assumed to be of greater relevance than the **purpose** (tourism, leisure, science) **assigned** to it by the disturber themselves (disturber’s point of view). While visitor **numbers** were found to matter (BURGER & GOCHFELD 2007, HOLMES 2004, NIMON 1997, more detailed analyses in THIS STUDY), differential visitor **conduct** has generally been reported to evoke greater differences in comportment (NIMON 1997, majority of analyses in THIS STUDY). It must be emphasised, however, that most studies restricted themselves to relatively small changes in visitor number (max. 3 or 5), while tourist groups may comprise up to 100 people.

As regards investigation of impact of **tourism**, NIMON’s (1997) and BURGER & GOCHFELD’s (2007) studies remain exemplary, for they were the ones to recruit ‘true tourist groups’ for their visiting experiments, and even though the obvious problems of standardisation are acknowledged, it should also be kept in mind that the stimuli offered were definitely closer to ‘touristic reality’ experienced by penguins than (standardised) pedestrian stimuli chosen in many of the studies conducted on impact of human visitation (e.g., GIESE 1998; GIESE & al. unpubl. data; HOLMES 2007). While all of the studies acknowledged this limitation, some of them pointed out that evidence of impact of 1 visitor indicated an even greater impact if numbers were increased, and results obtained by

Holmes (2004) on differing numbers of well-behaved visitors (1 vs. 5) do indeed support this supposition.

Whether the extrapolations suggested in some publications would turn out correct or not, however, these studies do provide ample evidence on potential impact of **scientific research** (as also reported in terms of effects on breeding success by, e.g., Giese 1996 and Woehler & al. 1994) which can apparently be effected even if research procedures do not include invasive methods.

While it is undoubtedly true that in terms of numbers of people, the general danger of 'the more the messier' exists, factors such as e.g., duration of exposure, tightness of group, noise level, and frequency or abruptness of movements, are suggested to additionally exert a complex and most probably **interconnected influence** on stimulus perception. To further complicate matters, stimulus perception is likely to also depend to an as yet unquantified extent on stimulus traits outlined in section 6.2.2 and 6.2.3 (i.e., valence acquired over the course of evolutionary history; valence acquired through increased intensity or degree of novelty of stimulus; valence acquired by individual or social learning).

6.2.6.4 Impact of Visitation vs. Habituation Potential

> "The reactions of birds in frequently visited colonies, in comparison with those rarely visited, revealed a limited amount of habituation to my presence." (Penney 1968, p. 90 on Adélie penguins, *Pygoscelis adeliae*)
>
> "Yellow-eyed penguins may habituate to short and consistent approaches, but appear unsuitable for unregulated tourist visits at nest sites. Individual differences in habituation potential to human disturbance can have fitness consequences and may lead to contemporary evolutionary change in the composition of breeding populations." (Ellenberg & al. 2009, p. 289)
>
> „[…] birds that are prone to stress (i.e. those that would show extreme responses to human presence), may have moved their nest site out of the Tourist area, lowering both the average density and the average hormonal response as a function of avoidance rather than habituation.“ (Fowler 1999, p. 147 on Magellanic penguins, *Spheniscus magellanicus*)

Concerning behaviour as well as heart rate, this study did not find evidence of Adélie penguins, *Pygoscelis adeliae*, habituating to the visits they were subjected to.

According to Immelmann & Beer (1989), **habituation** constitutes a stimulus-specific waning of response, i.e. the animal learns not to respond to something on finding that nothing significant is contingent upon its occurrence.

As stated previously (Aim III), the extent to which the same individuals responded on different days rather seemed to reflect 'current state of being' likely to be mediated by (observed) differences in behaviour displayed immediately prior to visitation as well as (assumed) differential exposure to conspecific and/or predatory pressure prior to pre-visit records. It was not in line with habituation (nor sensitisation[55], for that matter). Whether this was due to penguin-inherent factors, colony location, or an experimental design which did not particularly lend itself to encourage the process (with respect to continuous vs. intermittent presentation of stimulus, daily visits might have yielded results different from the ones obtained) thus remains open to speculation.

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[55] The 'opposite' of habituation is sensitisation (McFarland 2006, p. 179): Increase in the probability of a response resulting from repeated presentation of a biologically significant stimulus. The results of sensitisation are easily confused with those of conditioning, but sensitisation occurs in the absence of correlated reinforcement, and is a form of learning more akin to habituation.

Results from other studies highlight differences between species and possibly colony location (Culik & Wilson 1995); additionally differential habituation potential has been proposed with respect to continuity of stimulus presentation (Fowler 1999, Walker & al. 2006) as well as sex, personality, and previous (invasive) experience with humans (Ellenberg & al. 2009).

Wilson, R.P. & al. (1991) found behaviour of Adélie penguins to suggest habituation to human presence and movement (regularly passing the nest at a distance of 5 m), whereas heart rate upon approach showed substantial increases. Their finding might either indicate **differential response 'preferences'** (e.g., Duncan & Filshie 1979) or **different degrees of 'danger' perceived** with respect to tangential passing and direct approach (Burger & Gochfeld 1981, but see review by Fernández-Juricic & al. 2005 for lack of across-species consistency). The fact that no behaviour response was observed during *regular* passes at a *consistent* distance additionally suggests **predictability of stimulus exposure** to be an important factor.

Holmes & al. (2005/ 2006) found behaviour responses (increased 'vigilance', 'high vigilance', 'low threat/ display'; decreased 'rest') from **off-station** (nesting in a rarely frequented area) Gentoo penguins, *Pygoscelis papua*, to significantly exceed those of **on-station** (experiencing regular exposure to station personnel) penguins in both magnitude and post-visit persistence. Concerning Gentoo penguin comportment, Nimon (1997) raised the possibility of **within-season habituation** in penguins repeatedly subjected to visitation by groups of well-behaved people.

Ellenberg & al. (2006) **did not observe any habituation potential** with respect to Humboldt penguin, *Spheniscus humboldti*, heart rate responses during either three consecutive passes at 20 m distance or during repeated nest-checks; for the latter experiment, a reduced recovery time was found between first and second, but not second and third day. They considered persistent predation by humans (for the last 11,000 years) to be a likely selection force favouring 'survival of the timid'. Jouventin (1982, p. 95) likewise proposed artificial selection by man (in this case, overwintering sealers) to account for Gentoo penguins' differential degrees of shyness on different islands:

> "The hypothesis of the transmission of a 'traditional' fear of man seems unsupported, an artificial selection involuntarily made by sealers seems more likely: as the latter considerably reduced the island population, only individuals which fled from man were able to reproduce."

In contrast, behavioural and hormonal **habituation** to regular exposure to tourists has been described for Magellanic penguins, *S. magellanicus* (Fowler 1999, Walker & al. 2006), with the former author, however, pointing out the possibility of less stress-tolerant birds having vacated the area. This caveat appears to be supported by Hockey & Hallinan's (1981) finding of a complete absence of prospecting[56] African penguins, *S. demersus*, in a colony through which a single human had passed for several consecutive days. With regard to beach groups of African penguins, vanHeezik & Seddon (1990, p. 92) found "medium-term exposure to low-level non-contact human disturbance" to result in "**desensitization** of groups of penguins […] to further disturbance". They cautioned, however, that next to sufficient visitor distance (30 m) and regularity of exposure, penguin group size needed to be taken into account to minimise socially facilitated flight reactions (with larger groups more likely to contain more timid individuals).

Concerning Yellow-eyed penguins, *Megadyptes antipodes*, Ellenberg & al. (2009) reported **little habituation** in heart rate increases with respect to **maximum values**, but found **significantly reduced recovery times after** regular visits by a conscientious single human on **five consecutive**

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[56] pre-breeders, looking for a place to settle

days. Habituation potential, however, was significantly influenced by prior (invasive) experience with humans, as well as by character (calm birds habituating more easily than aggressive ones) and sex (females habituating more easily than males). Yellow-eyed penguins thus appear to be able to get used to short and consistent approaches, and might tolerate strictly regulated tourism (Ratz & Thompson 1999), but certainly do not cope with unregulated tourism (McClung & al. 2004).

As Immelmann & Beer (1989, p. 126) emphasise, **habituation** is **highly stimulus-specific**, and "a new stimulus, replacing the one to which response has become refractory, immediately reinstates the response at approximately full strength". Given the range of facets the stimulus of human visitation comprises (e.g., conduct incl. height of human 'over penguin', angle of approach, number of visitors, duration of exposure, tightness of group, noise level, and frequency or abruptness of movements), true habituation of penguins to anything but 'severely choreographed' human contact seems unlikely, and in this respect, increased numbers of people are suggested to increase the degree of 'unlikelihood'. Selective utilisation of differently frequented areas (i.e., more 'timid' penguins moving out of areas of more frequent human contact), in contrast, appears more probable, and consequences should be taken into account when deciding on visitor regulation.

6.2.7 Aim VI: Identification of Indicative Behaviours and Postures

> "For people visiting breeding kings, gentoos, and royals, identifying altered penguin behavior [sic] has some inherent impracticalities. For example, it would be impossible for visitors to identify decreased rest in an animal without some assessment of this behavior prior to visitation. During this study, no behavior could be reliably regarded as an exclusive response to pedestrian presence. However, certain behaviors appear likely to prove useful as indicators of modified penguin behavior in response to human activity." (Holmes 2007, p. 2580)

> "The larger the island of knowledge, the longer the shoreline of doubt – and the broader the drift-line of variation." (Trio inf., expanding upon R.W. Sockman)

6.2.7.1 Conclusions – Identification of Indicative Behaviours

Identification and classification of behaviours as indicative depends on **sampling methods** and **observer focus** (individuals, groups). A number of **penguin-inherent factors** (e.g., stage of breeding cycle, body condition, coping strategies, stimulus perception) as well as time of day, have to be taken into account if indicative behaviours are used to gauge impact of visitation.

With respect to penguin **groups**, easily identifiable indicative behaviours (i.e., behaviours for which at least the direction of change is equal in the majority of birds) appear limited to those strongly influenced by social facilitation, i.e., increased vigilance and decreased resting.

Examination of **individual** focal animals showed all comportment parameters analysed to be affected by human visitation, with different individuals changing different behaviours at different stages of the visit (s.b.), and choice of response behaviour to some extent dependent on pre-visit behaviour displayed and quality of stimulus presented (e.g., moving vs. non-moving). If this finding were to be incorporated into **guidelines for visitor conduct**, it might be easiest to advise people to be additionally attentive (i.e., while not losing sight of vigilance levels!) to increased switches between behaviours of individual penguins (within-subject 'scattering'), and to increased incoherence of comportment displayed by different penguins (between-subject 'scattering').

Concerning switches and incoherence, particular importance should be placed upon ‘more intense’ behaviours, with a tentative gradation suggested to run from resting (lowest intensity) via comfort and breeding, to vigilance and agonistic behaviours (highest intensity). Furthermore, detection of agonistic behaviours – directed against humans as well as conspecifics – should not be expected, but taken very seriously upon occurrence.

Recognition will be facilitated, particularly for tourists who usually visit different species, if introductory talks about guidelines refer to **videotaped accounts of** these **behaviours**, both as observed in **groups** (e.g., vigilance, increased incoherence), and in **individuals** (e.g., agonistics, increased switches between behaviours).

6.2.7.2 What Constitutes an Indicative Behaviour?

Given the fact that identification of indicative behaviours and their subsequent incorporation into comprehensive guidelines was one of the ‘applied’ aims, it is rather unfortunate that THIS THESIS found that **there are no ‘facile’ answers** to the question. Instead, results highlighted a number of problems and limitations of the concept itself. These will be explored, and a possible option to include these findings will be presented.

To be considered indicative, (changes in/ occurrence of) a given behaviour or posture should provide **reliable information** on a) the fact that an impact is perceived by the subject (qualitative; essential prerequisite), and b) the strength of this impact (quantitative; ultimately desirable, but initially optional).

Reliability of information provided, however, might differ depending on focus: If an **individual** was found to consistently respond to disturbance with a specific behaviour (or changes thereof), this behaviour would deserve to be classified as indicative. Within a **group** context, in contrast, individual animals might be observed to employ different coping strategies (within-animal consistency, between-animal disparity), with perhaps only one of these strategies related to that particular behaviour shown by the initially observed individual; alternatively or additionally, a group might represent a mixture of responsive and non-responsive (perhaps not yet responsive) animals. While all/ many of the responses shown would have been recognised upon focusing on the individual, the variety of responses observed in the group might lead to the conclusion that no indicative behaviour exists, or – worse – that there is no disturbance.

Detailed reference to behavioural/ postural changes reported by other researchers has been made in chapter 2.3.2.1.1, and findings particularly relevant to THIS STUDY have been revisited in section 6.2.2. Concerning Adélie penguins, *Pygoscelis adeliae*, literature (e.g., AINLEY 1974, 1978; JOUVENTIN 1982; PENNEY 1968; SLADEN 1958) as well as personal observations during the trial field season near Arctowski Station in SSSI 8 (1999) had identified several behaviours as sensitive to (human) disturbance, viz., an increase in vigilance (operationalised as ‘alert’ for focal groups), agonistic behaviours (‘agon’), displays and wing-flaps (‘roughly’ co-represented by ‘fl-up’ for focal groups), nest (and egg/ chick) manipulation (FA: ‘breed’, FG: ‘manip’), headshakes (‘head-shakes_yes’), and an upright posture (‘posture_up’) as well as a decrease in resting and ‘small’ comfort behaviours (e.g., yawn, bill-tremor) which were evaluated separately (‘rest’, ‘comfort’) for focal animals and captured jointly in the category ‘rest&Co’ for focal groups. While preening behaviour (FA: ‘comfort-preen’, FG: ‘preen’) had been explicitly stated not to change during human disturbance (AINLEY 1974), THIS AUTHOR’s own preliminary observations (reconnaissance field season) had suggested an increase after withdrawal of the stimulus.

These behaviours were subsequently examined, using different sampling methods (30 s Instantaneous Scan and One-Zero Sampling for focal groups, Continuous Recording and second-by-second transcription for focal animals) and subjected to analyses on different levels of complexity (focal groups, focal animal elements/ topography) to investigate each behaviours' relevance and sensitivity on these levels (FG: How many penguins respond at a given point in time? → ±consistency; FA: How many penguins respond per visiting stage? → consistency; How strongly do they respond? → magnitude of changes in prevalence; In what way do they respond, i.e., which changes in behavioural structure cause the changes observed? → 'syntax', composition).

6.2.7.3 What Do We See? – Choice of Sampling Methods, Sensitivity of Observer

Focal-group behavioural evaluations were designed to give an impression of whether the respective behaviour might serve as an **indicator for non-penguinologists** as well. If a given and 'fairly conspicuous' behaviour changes in a similar direction for most penguins (e.g., 'alert'), then an untrained person can be expected to pick up the clue and abide by it. If on the other hand, individuals change their behaviours in different ways (intensities or even directions); then the untrained observer is likely to get the wrong impression. In that case, it might be more useful to guide the eye of the beholder towards a more 'reliable' source of information for assessment of disturbance. Information obtained through **focal-animal evaluations** requires more time (data processing) and a more detailed knowledge on 'ethogrammatical' features of a given species, but is proposed to provide a **sound grounding for assessment** of degree of sensitivity of indicators suggested by less taxing methods.

During focal-group evaluations, increased vigilance and decreased resting could be readily identified as disturbance indicators on this rather general level, as these changes were displayed by the majority of the group members. Due to differing baselines for individual groups/ datasets, magnitudes of difference between periods (before, during, after visitation) constituted an important additional information to absolute intensities.

Responses in vigilance (increase) and resting behaviour (decrease) to human disturbance have likewise been reported in most published studies (see section 6.2.2). The majority of them were conducted on 'series of individual focal animals' (which were approached individually and results on which were later pooled) rather than focal groups, suggesting that the 'considerably cruder' sampling method employed in focal-group evaluations still remained sufficiently sensitive to reflect changes in vigilance/ resting behaviour. Particularly with respect to the category 'alert', but to a lesser extent also to the category 'rest&Co', the 'contagious' effect (social facilitation) of the behaviour seems to render them more amenable to focal-group sampling than the other categories.

The fact that for these parameters **magnitude of changes rather than absolute intensities** may be used to gauge the extent of penguin responsiveness makes them easier to assess for humans in general, and for short-term or untrained observers in particular. Concerning the problem of a **'lack of pre-visit baseline'** (see quote by HOLMES above), gradual approach was found to tally with gradually increasing response levels so that even if values for 'absence of disturbance' are missing, changes would still become apparent (successively more penguins successively more affected).

While reflecting on behaviours that went 'undetected' by focal-group evaluations, it has already been emphasised (section 6.1.3.1) that if untrained observers are advised to adhere to changes in resting and vigilance behaviour for gauging their impact, they should be simultaneously made aware of the fact that performance of other behaviours may also be impaired but that these changes are far less likely to be detected by them.

With respect to those categories for which changes were small or went undetected during focal-group evaluation, more detailed examinations (focal animals) suggested that lack of findings was mainly attributable to the fact that behaviours exhibited more rarely and/or by fewer subjects were less likely to show big differences in a group setting. Changes detected when more sensitive sampling methods were employed emphasise the severe limitations of easily applicable (and teachable) methods of gauging impact.

6.2.7.4 What Can a Penguin Do? – Stage of Breeding Cycle and Other Factors

> “The strength of an animal’s behavioural response to human presence has often been used as an index of an animal’s susceptibility to disturbance. However, if behavioural responsiveness is positively related to the animal’s condition, this may be an inappropriate index, as individuals showing little or no response may in fact be those with most to lose from changing their behaviour.” (Beale & Monaghan 2004b, p. 1065 on Turnstones, *Arenaria interpres*)

Response differences (observed distance of first response, readiness to flee) related to **stage of breeding cycle** and thus nest contents (eggs, small or large chicks) have been stated for, e.g., Adélie, *Pygoscelis adeliae* (Wilson, R.P. & al. 1991), African, *Spheniscus demersus* (Giese & al. unpubl. data), and Magellanic penguins, *S. magellanicus* (Cevasco & al. 2001). Authors agreed that a far stronger stimulus was needed to induce flight behaviour (often operationalised as increases in ‘posture_up’, taken as a precursor to movement away from disturbance) during incubation of eggs and brooding of small chicks (increased danger of predation) than if the chicks were larger or if the penguins had only to look after themselves. Furthermore, due to differences in breeding cycle, displays (ecstatic[57], mutual[58]) reported by various authors to constitute an unmistakable indicator of disturbance, were extremely rarely encountered in the datasets evaluated in THIS STUDY, but frequently found during monitoring nest checks in other colonies witnessed prior to and post-study (pers. obs.).

In other words, ***response repertoire*** available to penguins during incubation must be considered seriously ***curtailed*** with respect to expression of behaviours that would not leave a visitor in any doubt as to the disturbance they are causing. This **context-mediated lack of response** does by no means indicate, however, that these penguins are less disturbed.

Apart from the great inter-individual variability observed in the parameter ‘headshakes’, feeding a chick also considerably increased the occurrence of headshakes in parent birds. Headshakes became more frequent as chicks appeared (bending down, especially when feeding, seemed to increase the need to shake the head, i.e. clear the nose from salty liquids). Likewise, adoption of an upright posture increased as the chicks hatched. For such behaviours, a ***change in valence*** attributed to their performance (What do they do it for?) must be taken into account when proposing them as indicative of human disturbance.

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[57] The ecstatic display is performed mainly by lone males on the territory, functioning to advertise the nest-site to unpaired females, rarely by females. As THIS STUDY commenced when nest-sites had been established, few occurrences were recorded.

[58] Mutual display generally occurs between well-acquainted partners or between parents and chicks. As few change-overs were directly witnessed, this behaviour did not feature greatly in THIS STUDY.

Apart from stage of breeding cycle (which can be found out about prior to visitation), evasion or flight behaviour has been shown to be influenced by other factors, e.g., **time of day** (Burger & Gochfeld 2007: Emperor penguins exhibited less deviation from paths close to tourists as light conditions deteriorated) and **body condition** (propensity to desert nest increases with decreasing body condition during incubation; e.g. Cevasco & al. 2001). While the former can be incorporated in interpretation of behaviour, the latter will vary between individuals and is thus not amenable to general assessment.

As for agonistic behaviours – be they directed against humans or against conspecifics[59] during visitation – **inter-individual differences** have been discussed in section 6.2.1, leading to the conclusion that the absence of agonistic behaviour is not an indicator of absence of disturbance. In contrast, presence of agonistics is suggested to constitute a definite sign that the penguin is experiencing difficulties in coping with the situation, and human visitors should seek to remove themselves from the presence of such birds.

Last, but not least, individual differences in **stimulus perception** discussed in 6.2.4 are suggested to constitute a further confounding factor on the quest for reliable indicative behaviours.

6.2.8 Aim VII: Identification of Threshold Distances

> “A densely packed colony of Adélies may at first glance give the impression of indifference to human intrusion, but as I became more familiar with the birds, I could perceive that my presence affected their behaviour. Some shy birds moved away from me when I was as much as 30 metres distant; others showed no reaction at 6 meters. I lessened my influence on colonies with a slow approach from downhill.” (Penney 1968, p. 90)
>
> “In conclusion, this study provides good evidence from two unrelated species [Kittiwake *Rissa tridactyla* and Guillemot *Uria aalge*] that human disturbance effects are related to perceived predation risk. This risk, and therefore disturbance effects, varies both with distance from humans and the number of humans present. This understanding has important implications for visitor management in nature reserves and the current use of set-back distances to minimize disturbance effects. If set-back distances are to be used as a management tool they must be measured and set for the greatest anticipated visitor numbers, and a strict cap must be maintained on visitor numbers at the site.” (Beale & Monaghan 2004a, p. 341)

6.2.8.1 Conclusions – Identification of Threshold Distances

Identification of response distances undertaken by numerous studies indicates the **concept of threshold distances** to encounter several **problems**. These pertain to species- and site-specificity, as well as to differences with respect to stage of breeding cycle, and individual susceptibility (‘personality’, differential stimulus perception). Additionally, the comportment parameters employed in THIS STUDY showed differences with respect to distance at which **maximum responses** (i.e., change found in greatest proportion of all sessions analysed) were obtained: Proportions for increased heart rate peaked during visitor approach to 5 m, maximum values for increased occurrence of scattered behaviour, increased breeding behaviour and increased occurrence of posture changes were calculated during visitor stay at 5 m, whereas visitor stay at 3 m elicited the most consistent responses as regards decreased resting, increased vigilance, increased agonistic behaviour and increased occurrence of headshakes. Likewise, **onset of a marked increase in**

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[59] In King penguins, *Aptenodytes patagonicus*, Holmes (2007) reported an increase in agonistic behaviour directed against conspecifics which he attributed to a decrease in inter-bird distances effected by human visitation.

response (e.g., rest and vigilance: during visitor approach to 15 m, agonistic behaviour and occurrence of headshakes: during visitor stay at 15 m) differed among parameters (also see Aims I and II).

Whether considerably shorter response distances reported from **penguins 'used' to human presence** can be attributed to habituation or results from pre-study segregation effected by differential tolerance of said presence remains unresolved; an investigation of **causality** appears relevant with respect to design of future management measures.

Across species, distinct changes in behaviour, posture and heart rate were observed at substantially greater distances than nest desertion, and changes in comportment usually showed a more or less gradual increase with decreasing distance from disturbance, raising the question of which **criterion/ cut-off point** to use as an indicator for threshold distance determination.

Proposal of threshold distances is generally **influenced** by animal- (conservation) as well as people-related (tourism, leisure demands) considerations; unequivocal recognition of the need for and subsequent adherence to empirically confirmed threshold distances that accommodate the various penguin-related factors (e.g., species, site, time of breeding cycle, individual variation) will be difficult to achieve but should be given high priority.

As mentioned above, heightened vigilance and decreased rest occurred during visitor approach to 15 m in more than half of the sessions examined in THIS STUDY. These behaviours were additionally found to be most easily recognisable, most probably even by a non-trained observer (cf. focal-group evaluations), indicating an **increase of threshold distance to a minimum of 15 m** (currently 10 m, e.g., UBA 2009) to be **warranted and feasible** with respect to breeding Adélie penguins. It is acknowledged that this result **cannot be extrapolated** to other penguin species, which may respond at an even greater (or lesser?) distance. Furthermore, inclusion into existing guidelines – though possible due to easy recognition of behaviour – **might not be welcomed** by tour operators and/or scientists, as adherence to such a distance might impede access to interesting features/ study grounds beyond a penguin colony (pers. obs., e.g., for tourism: Gentoo penguins at Hannah Point, Livingston Island, South Shetland Islands).

A change in terminology is suggested to increase awareness of welfare-conscious visitors as regards their potential impact, with **penguin-mediated threshold distances** determining the distance to visitors chosen by those **birds free to move** away (currently not incubating), and the term **minimum tolerance-distance** employed with respect to **incubating birds** for whom response repertoire to (and hence controllability of) disturbance stimuli is seriously curtailed.

Following, results pertaining to the question of threshold distances will be discussed in detail.

Response distances reported in the literature indicate a high degree of **species**- (e.g., BLUMSTEIN & al. 2005; ELLENBERG & al. 2004, 2006, 2007; HOLMES & al. 2005) and **site-specificity** (e.g., COBLEY & SHEARS 1999; HOCKEY & HALLINAN 1981; HOLMES & al. 2005/ 2006; PATTERSON & al. 1996; RATZ & THOMPSON 1999; WALKER & al. 2005), as well as differences pertaining to **stage of breeding cycle** (e.g., WILSON, R.P. & al. 1991; GIESE & al. unpubl. data; CEVASCO & al. 2001). **Individual-specific differences** are not yet as abundantly acknowledged (but see BEALE & MONAGHAN 2004b; DEVILLIERS & al. 2005; and particularly ELLENBERG & al. 2009 and references therein).

To provide the reader with an overview as to the complexity of the issue, **response distances** found in the literature and results obtained by visual appraisal[60] in THIS STUDY are listed from greatest

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[60] With respect to THIS STUDY, only results concerning a third and more sessions are included in the list

to smallest distance. Due to the drastically deviating results reported with respect to Gentoo penguins, study location is additionally mentioned for this species. Subsequently, a **synthesis** of the information is attempted, followed by reflections on the **purpose** of threshold distances.

6.2.8.2 Response Distances – Who Responds When to What and How?

As becomes obvious in the following passage, most studies have examined penguin responses to humans at a distance of less than 20 m, and particularly, less than 10 m.

6.2.8.2.1 List of Response Distances Reported

Responses to Humans at a distance of more than 100 m

- In ***Humboldt penguins***, *Spheniscus humboldti*, heart rate responses were measurable even to a single person **passing at 150 m distance** from the nest (ELLENBERG & al. 2006).

Responses to Humans at a distance of more than 30 m

- Average notice distance (penguins observably aware of people) for ***Emperor penguins***, *Aptenodytes forsteri*, passing groups of ('stationary') visitors was **36 m** (BURGER & GOCHFELD 2007).

Responses to Humans at a distance of 20 to 30 m

- No statistically significant changes in incubating ***Adélie penguin*** mean resting heart rate (82.4 bpm ±11.7), time spent prone, performance of vigilance and agonistic acts, and headshakes were found during **approach to** and subsequent **stay at 30 m** by a single person (GIESE 1998).
- If there were no visitors within about **30 m** of a crossing point (waiting tourists, approaching penguins), ***Emperor penguins*** usually continued their travel uninterrupted (BURGER & GOCHFELD 2007).
- If beach groups of ***African penguins***, *Spheniscus demersus*, were **approached** by a single person **beyond** a distance of **30 m**, alert and agitated behaviour increased greatly, regardless of prior history of disturbance (VANHEEZIK & SEDDON 1990).
- Average start of deviation distance (starting to change their direction of approach in response to people) for ***Emperor penguins*** passing groups of ('stationary') visitors was **23 m** (BURGER & GOCHFELD 2007).
- In ***Humboldt penguins***, average stand-up distance during direct **approach** by a single person was **20.2 m** (range: 7 m-50 m; ELLENBERG & al. 2006).

Responses to Humans at a distance of 15 to 20 m

- In ***Adélie penguins*** examined in THIS STUDY, **approach to 15 m** elicited decreased resting behaviour (55 % of all sessions), increased vigilance (51 %) and increased heart rate (37 %).
- Commuting ***Adélie penguins***, *Pygoscelis adeliae*, deviated by 70 m to avoid a single human **at 20 m distance** from their original pathway (WILSON, R.P. & al. 1991).
- ***Humboldt penguins*** exhibited distinct heart rate responses to single-person **passes at 20 m distance** from the nest (ELLENBERG & al. 2006).
- For ***African penguins***, average distance at which behaviour was altered during approach of 3 visitors was **20 m** (range: 5 m-41 m; GIESE & al. unpubl. data).
- ***Gentoo penguins*** breeding at a small, undisturbed Hope Bay colony will abandon their nests when **approached** slowly **to 20 m** by a single human (CULIK & WILSON 1995).

- Cuverville Island ***Gentoo penguins***, *P. papua*, approached by a larger group of 15 or more visitors adopted alert postures (65 %), beginning when the group had **approached to** a **15-20 m distance** (Nimon 1997).

Responses to Humans at a distance of 10 to 15 m

- In ***Adélie penguins*** examined in this study, occurrence of resting (57 %) and vigilance (53 %) responses increased further, while occurrence of heart rate responses decreased (i.e., increased heart rate shown in 'only' 24 % of all sessions) during visitor **stay at 15 m**.
- ***Adélie penguin*** mean resting heart rate (82.4 bpm ±11.7) increased to 96.4 bpm (±4.7) upon **approach to** and subsequent **stay at 15 m** by a single person. Time spent prone was less than during visitor approach to 30 m, and performance of vigilance and agonistic acts as well as headshakes increased, but differences were not statistically significant as compared to pre-visit levels (Giese 1998).
- For ***African penguins***, average distance of 3 visitors from temporarily vacated nests was **13 m** (range: 3 m-40 m; Giese & al. unpubl. data).

Responses to Humans at a distance of 5 to10 m

- Adult ***African penguins*** subjected to a **gradual** [step-wise, interspersed with pauses] **approach from 60 m to 10 m** exhibited a steady decline in birds lying down, and no chicks were lying down when the single person had reached 10 m (Hockey & Hallinan 1981).
- In ***African penguins*** subjected to a single-person **direct approach from 60 m to 10 m**, a complete cessation of preening was observed; additionally, birds previously prone stood up, and more than half the adults and chicks abandoned the colony (Hockey & Hallinan 1981).
- Only 4.7 % of ***Adélie penguins*** were standing after slow **approach to** and subsequent **stay at 10 m** by a single person; the "remainder were quietly incubating eggs and thus were undisturbed" (Ainley 1974, p. 17).
- A watching ***Adélie penguin*** would perform rapid-wing-flaps, ruffle-shakes, or both-wings-stretches when an intruder (human or skua) had come to **5-10 m** (Ainley 1974).
- For ***Emperor penguins*** passing groups of visitors, median crossing distance (while displaying changed behaviour) was **8 m** (Burger & Gochfeld 2007).
- Nesting ***Adélie penguins*** fled at an **approach** distance of **6.1 m** when the brood consisted of large chicks (single person; Wilson, R.P. & al. 1991).

Responses to Humans at a distance of 5 m

- In ***Adélie penguins*** examined in this study, **approach from 15 m to 5 m** further augmented occurrence of decreased resting (65 % of all sessions) and increased vigilance (58 %); it elicited the most cohesive response in terms of increased heart rate (80 %). During visitor **stay at 5 m**, decreased resting behaviour was found in 83 % of all sessions, increased vigilance was observed in 75 %, while increased heart rate occurred in 45 %. Additionally, increased occurrence of scattered behaviour (46 % = highest value during-visit), breeding behaviour (35 % = highest value during-visit), headshakes (38 %), and posture changes (39 % = highest value during-visit) were noted at this stage.
- ***Adélie penguin*** mean resting heart rate (pre-visit mean: 82.4 bpm ±11.7) rose to 126.3 bpm (±5.8) during **approach to** and subsequent **stay at 5 m** by a single well-behaved visitor. Approach also significantly interrupted incubation behaviour, with 68 % of the birds standing up, and a significant increase in vigilance and agonistic acts as well as occurrence of headshakes was observed (Giese 1998).

- In ***Royal penguins***, *Eudyptes schlegeli*, vigilance (at 20.9 acts per min) and heart rate (at 1.7 times resting heart rate) rose during **approach** and peaked when the single pedestrian **reached 5 m** (HOLMES & al. 2005).
- Most incubating ***African penguins*** demonstrated agonistic behaviour when 3 visitors **approached to** and subsequently **stayed at 5 m** (GIESE & DEVILLIERS 2004).
- Cuverville Island ***Gentoo penguin*** behavioural response as measured in proportions of birds adopting an alert 'posture' [sic] showed a marked reduction (65 % to 49 %) when a larger group of 15 or more visitors had **reached** the **5 m** distance and did not approach any closer (remaining at 5 m; NIMON 1997).
- For Macquarie Island ***Gentoo penguins*** breeding in an area of high human activity, behaviour displayed during a single-person **approach to** and subsequent **stay at 5 m** was not (statistically) significantly different from pre-approach behaviour (HOLMES & al. 2005/ 2006).
- Macquarie Island ***Gentoo penguins*** breeding in an area of low human activity displayed significantly higher levels of vigilance and low threat/ display behaviour and significantly lower levels of resting behaviour during a single-person **approach to** and subsequent **stay at 5 m** (HOLMES & al. 2005/ 2006).
- All ***Emperor penguins*** passing groups of visitors within **5 m** stood up some of the time to watch (BURGER & GOCHFELD 2007).

Responses to Humans at a distance of 3 to 4 m

- ***Adélie penguin*** heart rate almost doubled (from 76 bpm to 135 bpm) when the currently not incubating penguin was approached by a single human slowly walking **from 50 m to 4 m** (over 4 min), with the increase being slow to wane (from 135 bpm to 126 bpm after 2 min and penguin-imposed – the penguin moved away – increase in distance to 8 m; WILSON, R.P. & al. 1991).
- ***Adélie penguin*** heart rate rose from 126 bpm (s.a.) to 140 bpm upon further slow re-approach **from** said **8 m to 3 m** (over 1 min; WILSON, R.P. & al. 1991).
- Nesting ***Adélie penguins*** **approached** by a single person **to** within **3 m** seemed behaviourally undisturbed: They exhibited head movements (= increased awareness), but rarely threatening behaviour or escape (CULIK & al., 1989, 1990).
- In ***Adélie penguins*** examined in THIS STUDY, **approach from 5 m to 3 m** caused decreased resting in 78 %, as well as increased vigilance and heart rate in 64 % and 62 % of all sessions, respectively. During visitor **stay at 3 m**, the most cohesive responses in decreased resting (85 %) as well as increased vigilance (81 %), agonistics (33 %), and occurrence of headshakes (44 %) were observed. Increased heart rate was found in 42 %, and increased scattering in 43 % of all sessions.
- Cuverville Island ***Gentoo penguins*** **gradually approached to** within **3 m** from the nest (single, well-behaved visitor) exhibited brief spells of alert 'posture', but did not show a statistically significant heart rate response. During visitor **stay at 3 m**, neither heart rate nor behaviour was statistically different from pre-visit levels (NIMON 1997).

Responses to Humans at a distance of less than 3 m

- The frequency of ***Adélie penguin*** headshakes almost doubled when the single observer was standing at **2 m** from the colony edge after having stood at 10 m (AINLEY 1974).
- For ***Humboldt penguins***, the strongest heart rate responses were obtained during a **direct approach** of a single person **to** within **2 m** of the nest site (nest-check experiment), with heart rate increasing to 198 % resting heart rate (average: 104 bpm, range: 65-142 bpm; ELLENBERG & al. 2006).

- Nesting ***Adélie penguins*** fled at an **approach** distance of **1.3 m** when the brood consisted of small chicks (single person; Wilson, R.P. & al. 1991).
- ***Magellanic penguins***, *Spheniscus magellanicus*, nesting in isolated (isolated area) and 'scientifically' disturbed areas (study area) exhibited high levels of agonistic behaviour (alternate stares) during single-person **approach to** and subsequent **stay at 1 m**, whereas birds breeding in an area frequented by tourists (tourist area) showed significantly lower levels. Additionally, isolated and study area birds, but not tourist area birds, responded hormonally to human presence (increases in circulating corticosterone compared with basal levels; Fowler 1999).
- ***Gentoo penguins*** breeding at Ardley Island very near a summer station can easily be **approached** by a single human **to** within **1 m** without inducing nest abandonment (Culik & Wilson 1995).
- Cuverville Island ***Gentoo penguins*** subjected to a **brisk approach to** and subsequent **stay at 0.75 m** of the nest exhibited substantial, lasting heart rate increases (mean increase: 50.5 bpm, SE: 17.7) and adopted an alert 'posture' throughout the visit.
- Nesting ***Adélie penguins***' flight distance was reduced to **0.3 m** if they were incubating eggs (single person; Wilson, R.P. & al. 1991).

6.2.8.2.2 An Attempted Synthesis

Several aspects appear relevant in the context of threshold distances for penguins.

As discussed for indicative behaviours (see Aim VI), there is a substantial difference in responses obtained from **penguins 'tied' to their nests** (particularly if these contain eggs or small chicks) and those unencumbered in their expression of violated minimum-distances, i.e., **freely moving birds**. While being in one's own territory may to some extent change perception of stimulus and increase ability to cope, this appears to mainly apply with respect to outcome of intra-specific aggression. In incubating penguins, necessity to remain on the nest during disturbance is suggested to predominantly increase uncontrollability of stimulus and reduce the scope of behaviours available for coping (e.g., Broom & Johnson 2000).

Threshold distances depend to some extent on the **comportment parameter** chosen: In this study, the highest values for increased scattering (46 % and 44 %, resp.) were found at 5 m and at 3 m distance from the focal animal's nest, followed by that during visitor retreat (36 %); they were considerably lower during approaches to these distances (24 % and 27 %, resp.), and scattered behaviour occurred in more sessions during retreat (36 %) than during either of the approaches. The impression of scattering was often caused by the bird's inserting breeding behaviours into others (e.g. resting or vigilance). With moving stimuli being more likely to elicit unmitigated vigilance, scattering is thus far more likely to be observed during a visitor's stay at a given distance following an approach. Heightened level of scattering during retreat, on the other hand is assumed to be linked to a perceived waning of the disturbance stimulus. In this study, focal-animal evaluations indicated that in more than 50 % of all sessions appraised (n=51), decreased resting and increased vigilance were identifiable during approach to 15 m already (accompanied by heart rate increases in more than a third of all sessions), suggesting that **current guidelines for penguins in colonies** (e.g., UBA 2009: 10 m) **might be too lenient** to really accommodate the penguins' need (and thus rather reflect – in a number of locations – practical considerations as to possible pathways to 'interesting features' beyond penguin colonies).

Contrasting responses from on-station (regular exposure to station personnel) vs. off-station (rarely frequented area) breeding penguins (Holmes & al. 2005/ 2006) as well as from birds in tourist-area vs. irregularly, rarely or 'never-before visited' area (Fowler 1999), may indicate a capacity for **habituation** (as also proposed by Walker & al. 2005), but might be partly or entirely due to pre-study **segregation by previous disturbance** (as also suggested by Ellenberg & al. 2006), with birds intolerant to it no longer breeding in the area. The resulting lack of adverse response in 'habituated' birds might be considered positive regardless of cause, but design of future management measures (e.g., more birds exposed to fewer people vs. fewer birds exposed to more people) cannot disregard the difference.

Approach experiments including visitor stay at several distances greater than the 'rule-of-thumb' 5 m threshold distance provide ample evidence for **distinctly altered behaviour and increased heart rate** in incubating birds at 15 to 20 m (Adélie, some Gentoo), 20 to 30 m (Emperor, African), or even considerably further away (Humboldt). Most or all of these behaviours appear increasingly affected as the visitor moves in closer; additionally, more behaviours are altered in a greater number of penguins upon closer approach. In this study, for instance, increased agonistic behaviour was observed in progressively more sessions from each visiting stage to the next: After an initial rise from 2 % during approach to 15 m to 17 % during stay at that distance, proportions peaked during visitor stay at 3 m (one third of all sessions, n=39), and dropped markedly (to 7 %) only when the visitor retreated.

If, in contrast, (imminent or actual) **nest desertion** is taken to be the relevant criterion, threshold distances reported are generally substantially reduced (s.a., Adélie penguins: 0.3 m when incubating).

Adoption of any type of **threshold distance** thus appears to depend not so much on the fact that disturbance is experienced by the birds, but on the **human-made decision of extent of disturbance deemed acceptable**.

6.2.8.3 The Purpose of Threshold Distances

> "Our study also used an approach distance, but it was a penguin-mediated approach distance, rather than a tourist-mediated one. That is, we observed how close the penguins would approach us before changing their behaviour, rather than the other way around." (Burger & Gochfeld 2007)
>
> "We consider minimum approach distance guidelines should be based on the separation distance necessary to allow animals to undertake normal activity, rather than on the distance people can approach wildlife before the animals flee." (Holmes & al. 2005, p. 339)

In wildlife management, threshold distances, minimum approach guidelines, and buffer areas are proposed to reduce human impact on animals (Fernández-Juricic & al. 2005; Holmes & al. 2005). If this management is 'financially disinterested', the main consideration concerns the level on which impact is to be measured e.g., in terms of colony or individual breeding success (toleration of loss of peripheral nests to a certain extent), or recruitment of prospecting birds (with possibly lower site-tenacity).

If, however, a threshold distance additionally needs to accommodate people eager to watch the animals/ use the area, further considerations are suggested to come into play. The **generic terrestrial minimum approach distance (5 m)** advocated for almost all Antarctic species has long since been criticised (e.g., Workshop on 'Human Impact on Antarctic Mammals and Birds'. Institut für Polarökologie, Jena, 04/ 05 May, 1998), and IAATO (2007) has somewhat amended it to 5-10 m (with decision supposedly up to the individual visitor or tour guide) for nesting seabirds.

Its tenacity appears to be largely due to the fact that in ‘touristic practice’, at a number of sites visited, it is not always possible to maintain the prescribed distances (let alone greater ones) due to terrain or narrow access to features of interest (Davis 1999, Enzenbacher 1992a). Even though this problem is likewise encountered by scientists (e.g., passing through an area to reach their site of research, pers. obs.), the numerical implications are far more substantial with respect to tourism (max. 100 people landed conjointly, with bigger ships landing several loads of people in succession).

Adoption of a single sensitive **threshold distance** that ‘caters for the most vulnerable’ (period/ breeding stage/ individual), would certainly be deemed unacceptable by most visitors and tour operators alike (and possibly Antarctic annual residents as well). Unequivocal recognition of the need for and subsequent adherence to empirically confirmed threshold distances that accommodate the various factors (e.g., species, site, time of breeding cycle, individual variation) should therefore be given high priority.

In the meantime, a change in terminology might help sensitise visitors interested in animal welfare to this problem: **Penguin-mediated threshold distances** as proposed and utilised by Burger & Gochfeld (2007) ought to be considered the minimum distance to minimise stress to non-incubating birds, even though these authors as well as Beale & Monaghan (2004b) caution that external factors like fading daylight and individual-related factors like body condition might invalidate generalisation of such thresholds to some extent. In consequence, distance measures obtained from birds free to move away at will are suggested to constitute a critical threshold the crossing of which will cause incubating birds to experience an increasing motivational conflict between guarding their nest and moving away. Any distance beyond had best be more honestly termed a **minimum tolerance-distance** and should be acknowledged to vary according to numerous factors generally outside the control of an incubating bird.

6.2.9 Summary for Non-Penguinologists – Human Visitation and Penguin Welfare

So, what about penguin welfare? Do penguins ‘mind’ human visitation?

This study found a clear behavioural response in the majority of individuals, while heart rate of at least some of the birds appears to have been remarkably resilient. With respect to behaviour and to a lesser extent heart rate, findings thus indicate a definite short-term detrimental effect, but do not make a convincing point with respect to long-term negative consequences. So we might rest assured and open our arms to visitors (be they scientists, station personnel or tourists) – except for a couple of noteworthy ‘asides’ some of which are quite indirectly related to this study.

In those cases where change-overs could be directly recorded, heart rate of penguins coming back from the sea was elevated and showed a slow, steady decrease/ recovery. In contrast, heart rate during human visitation (and other human disturbances) exhibited a much greater and much more erratic variation.

Human disturbance comes on top of everything else – for the colony investigated, this includes conspecific disturbance and predator pressure as well as climatic changes which challenge the Adélies by making the area more amenable to Gentoo and/or Chinstrap penguins. These impacts are interwoven and jointly influence the penguins’ welfare (as well as their fitness), and while ‘additivity’ may be assumed, the ‘whole disturbance’ is quite probably more than the sum of its components.

Welfare looks at the individual – and those individuals who do show changes leave the onlooker in little doubt as to their being disturbed. Adélie penguins have been found to be among the most ostentatiously expressive of all penguins – quite the opposite to, e.g., Emperors. So while heart rate responses without behavioural correlates were quite rare, the opposite was observed fairly frequently. But being so behaviourally 'outspoken' also appears to make them prime candidates for rash actions which in turn might lead to consequences at least equal to prolonged elevated heart rate (which Regel & Pütz 1997 have mathematically shown to result in energy loss necessitating extra food rations and which has been linked to immune system deficiencies, and other long-term detrimental consequences); viz., spontaneous nest desertions which, even if only temporary, quickly result in loss of eggs or young chicks due to exposure/ predators.

Welfare looks at the individual's capacity to cope as regards their environment. Do Adélies cope? How can we know that the ones who appear to do so are not the ones left over, i.e., have we already arrived past 'weeding season'? This study did not encounter exactly the same nests for two successive seasons – even though groups were delineated within some metres of last year's area. While this may be partly due to the fact that edge nests are subjected to a number of location-inherent problems which, by the way, are usually borne by couples with lesser breeding experience, it is again suggested that human disturbance adds yet another factor to make penguin life more difficult and penguin breeding success more unlikely.

While the actual breeding colonies of Adélie penguins are mainly subjected to disturbance by scientists (and, depending on location, station personnel), landing beaches are often areas on which tourists are allowed to crowd (as mentioned above, up to 100 passengers may be landed at the same time, and larger ships have been known to appropriate a beach for up to six successive hours, pers. obs.). In these cases, penguins either choose to postpone their landing, which might lead to irregularities in change-over during incubation and might impact on chick-feeding after hatching, both of which can have detrimental effects on breeding success. Alternatively, penguins will land further away; concerning commuting birds (travelling between sea and colony), Wilson R.P. & al. (1991, p. 368) found a single observer 20 m from a well-travelled penguin path to cause an estimated 11,934 birds to deviate during 10 h, resulting in "an extra 835 penguin kilometres walked".

It is therefore strongly suggested that most **Adélie penguins do 'mind' human visitation** (whatever its purpose) and their welfare does consequently suffer. Concerning the probability of Adélie penguins 'getting used' to humans, it is concluded that most of the necessary prerequisites for 'habituation' (regular, consistent exposure to a relatively invariant stimulus) cannot be met, partly due to the penguins' breeding biology (penguin-mediated; several months at sea each year, longer[61] incubation shifts for each partner), and partly to human inability to achieve an invariance[62] in stimulus (people-mediated; e.g., nest monitoring by few people vs. presence on the beach by many). While in a long-lived, relatively frustration-tolerant species (skuas and climatic havoc will lead to brood-failure even in the absence of humans), consequences may take a long time to become obvious to our eyes/ scientific evaluation methods, caution is warranted as the Adélie penguin must be considered 'multiply challenged', with 'new' disturbances being added to the 'old (evolutionarily adapted to) evils'.

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[61] In this respect they differ from Gentoo penguins (daily change-overs), but not from Magellanic penguins, for whom in recent times the greatest body of evidence in favour of habituation has been presented, predominantly based on the penguins at Punta Tombo (e.g., Yorio & Boersma 1992; Walker & al. 2005, 2006), but see Fowler (1999).

[62] This might explain habituation effects presented with respect to Yellow-eyed penguins at Pipikaretu Beach, N.Z. (Ratz & Thompson 1999, pers. obs.), but not elsewhere (Ellenberg & al. 2007; McClung & al. 2004), also see Ellenberg & al. (2006) for a caveat.

6.3 Prospects for the Future

Next to the facts that human visitation does impact on penguin comportment (i.e., behaviour, posture, and heart rate), and that this impact was detectable in all comportment parameters examined, the most relevant finding of THIS STUDY relates to inter- and intra-individual differences obtained by observing the same pool of individuals over successive days/ weeks. The **Modulation Model for Individual Response Differences** (fig. 6-1) draws attention to the variety of levels on which behaviour observed at a given point (or period) in time is influenced prior to, during, and after stimulus presentation. Even though this model still does not capture the complete picture, it serves to emphasise the impossibility of 'keeping constant all parameters but one' to assess a given parameter's influence within context, let alone quantify its interaction potential.

To date, one **pragmatic approach** to this complexity has been to *a priori* standardise stimulus presentation with respect to the stimulus itself (e.g., same visitor, same clothing, same type of approach), biotic and abiotic conditions (e.g., predator absence, same weather conditions), and experimental group (e.g., stage of breeding cycle, nest location) to minimise variability as much as possible (e.g., studies by GIESE & al., HOLMES & al.). By and large, presentation of results further reduced variability by reporting, e.g., SE-values (which, after all, refer to deviations from the hypothesised true mean of the entire population, and not to the group of individuals actually examined – whose variability would be captured in SD-values) and focusing on mean responses. By explicitly co-presenting the extent of variability whenever averages were provided, THIS STUDY highlighted that such summarising values rarely adequately reflected 'individual reality'. Moreover, the construct of 'individual reality' is proposed to result from a complex interplay of external and internal factors, with the latter constituting a considerably elusive residual not easily accommodated in research design.

Back to the 'black box', then? This opposite extreme can hardly be recommended, as 'losing oneself in the avalanche of information provided by each individual' will not help to generate publicly acceptable statements (e.g. for guidelines).

Instead, it is proposed that a **shift in approach** is needed, as neither THE penguin response nor THE human disturbance stimulus does exist. Penguin individuality turns out to be a worthwhile field of research, particularly with respect to adaptive capacity and thus potential endurance of human interference.

Conscious **inclusion of and reports on variability** (i.e., explicit focus on inter- and intra-individual variability) are suggested as an interim compromise, because these do not negate individuality, but channel it into analytically manageable units. In that context, ELLENBERG & al.'s (esp. 2009) approach, i.e., classification according to penguin personality type, sex, and previous experience with humans, appears the currently most feasible way to include some of the **penguin-inherent factors** in the model.

Findings from THIS THESIS additionally point to **environment-mediated intra-individual response 'preferences'** (heart rate vs. behaviour, different behaviours); developing ways to explicitly accommodate these might further our understanding of **response flexibility within a given personality type**, and thus help with the interpretation of observed variability. Inclusion of these findings into, e.g., ELLENBERG & al.'s 'personality-mediated typology' appears a viable option for research in the foreseeable future.

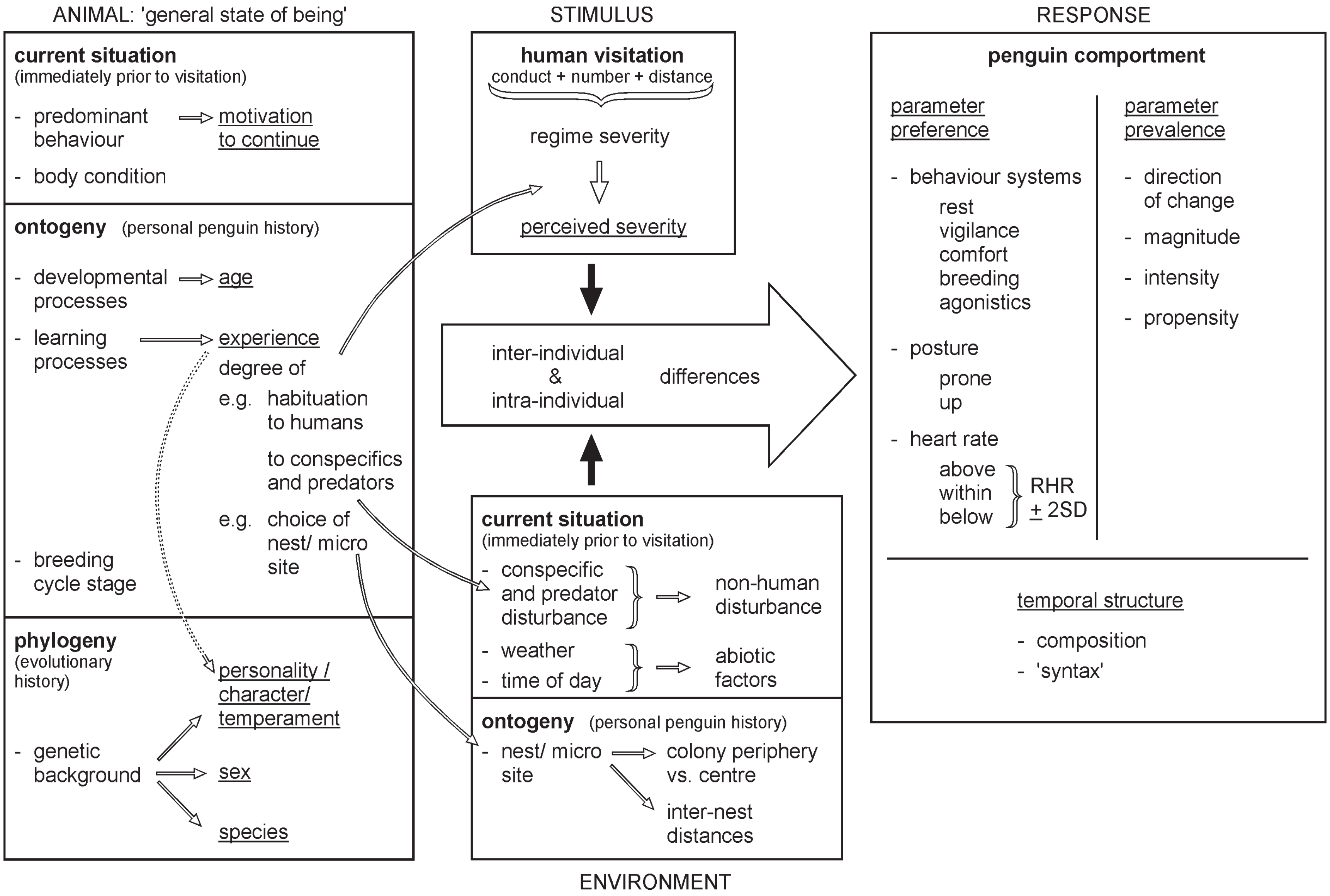

Fig. 6-1: Modulation Model for Individual Response Differences. Animal-inherent, stimulus- and environment-mediated factors as well as their (inter-)actions contribute to inter- and intra-individual differences in observable/ measurable penguin comportment. RHR: resting heart rate; comportment: behaviour, posture, and heart rate.

7 Summary/ Zusammenfassung

7.1 Summary

The STUDY PRESENTED HERE provides qualitative and quantitative evidence on existence and extent of incubating Adélie penguins' behavioural and heart rate responses to human and conspecific disturbance, and additionally reports observations on disturbance by predators and aircraft noise.

- Over the past two decades, **wildlife in the Antarctic Peninsula region** has been increasingly subjected to two major challenges, viz., global change and human presence (tourism, leisure, and science). As global change is unlikely to be redressed in the foreseeable future, human conduct becomes the only 'adjusting screw' available to reduce overall impact.
- Visitors to the Antarctic particularly enjoy human-penguin encounters. **Adélie penguins** (*Pygoscelis adeliae*) were chosen for this investigation, because their behaviour repertoire is well documented and they are among the most ostentatiously expressive of all penguins. Furthermore, Adélie penguins are classified as 'least concern' (IUCN Red List), and at the same time as 'susceptible to human disturbance'. **Incubating penguins** were favoured over freely moving ones, because in nest-bound birds heart rate measurements are less confounded by locomotor activity (study design). Moreover, these penguins cannot evade human visitation without endangering their nest contents, which limits their chances for coping and renders them particularly vulnerable to human interference (animal welfare).
- THIS THESIS combined **two objectives**:
  1. A thorough and comprehensive **quantitative analysis of extent of impact** of human visitation was undertaken to gauge proximate consequences for animal welfare and assess potential ultimate fitness repercussions.
  2. To contribute to the development of tenable, effective concepts for conservation and the formulation of penguin-sensitive **guidelines for human conduct**, the outcome of rigorous but labour-intensive 'high resolution' evaluation processes was compared with those of more expeditious methods, and analyses were complemented by reflections pertaining to applicability of findings.
- To this end, **visiting experiments in the field** were conducted during the second halves of two incubation periods (mid- to end of November until beginning of December) of two consecutive years (2000, 2001) on King George Island, South Shetland Islands, in maritime Antarctica. The data analysed were collected at SSSI 13 – now ASPA 132[1] – 'near' the Argentine Station 'Jubany' following a reconnaissance field season at SSSI 8[2] – now ASPA[3] 128[4] – near the Polish Station 'Henryk Arctowski' in 1999. At both locations, Adélie penguins were not subjected to touristic visitation directly at the colony.
- A total of **five penguin groups** (10 to 48 incubating members, median = 22.5) plus a varying number of currently mobile conspecifics were examined. Of these groups, a **total of 23 penguins** were included in **focal-animal** analyses. One penguin group did not receive any visitation (2000); the others were subjected to **four standardised visiting regimes**.
- Impact was assessed using a combination of **ethological and physiological parameters**:

  Penguin **behaviour s.l.** ('dependent variable') was recorded on video tapes – along with information on three different **types of disturbance**[5] ('independent variables'). **Penguin heart**

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[1] Potter Peninsula, King George Island (=Isla 25 de Mayo), South Shetland Islands, Maritime Antarctic

[2] SSSI = Site of Special Scientific Interest

[3] Antarctic Specially Protected Area (q.v.)

[4] Admiralty Bay, King George Island (=Isla 25 de Mayo), South Shetland Islands, Maritime Antarctic

[5] viz., conspecific, predator, and aircraft disturbance (human disturbance being subject to diligent note-keeping)

rate of selected focal animals was measured by placing artificial eggs with an infrared sensor into their pebble nests.

- **Sessions** were recorded on video, with each of the **'visited' sessions** comprising **three periods**, viz. 'pre-, during- and post-'visitation. These were complemented by so-called **'baseline' sessions,** i.e., recordings without human visitation. Thus, data include recordings of entirely undisturbed penguins, penguins disturbed by conspecifics and/or predators, and penguins subjected to visitation experiments. In concordance with the dual objective of the study, data were evaluated at **two 'resolution levels'**: A **total of 30 sessions** examined entire **focal groups** = 'FG', while data on individual **focal animals** = 'FA' were transcribed for a **total of 119 sessions**.
- The **results presented are based on a total** of
  - approximately **90** incubating **penguins**, **23** of which featured as **focal animals**
  - **47 h** (= 169,200 s) **video** recordings (of 119 sessions)
  - **9,315 units** of **heart rate** recordings (20s-intervals of 88 sessions)
- In concordance with Objective No. 1, an **individual-based, minimally-intrusive research approach** was chosen. Intrusion was inevitable during placement of the artificial egg, and paint marking the respective bird permitted distinction from their naïve partners and hence quantification of inter-individual differences. Observations of the same individuals on different days provided insight into intra-individual differences.
- Pair-wise comparison of the three visiting periods – and additionally with equivalent time-spans of unvisited sessions ('baseline'; heart rate only) – were effected to **quantify**

  a) **immediate impact** during stimulus presentation (during-visit vs. pre-visit)

  b) **continuation/ waning of responses** after stimulus withdrawal (during- vs. post-visit)

  c) extent of **recovery** (post- vs. pre-visit).

  d) spontaneous/ natural variation ('baseline').

  Attention was given to inter-individual differences in response **propensities** of individuals. Behaviour s.l. and heart rate parameters were analysed as regards **prevalence** (predominance, occurrence, absence), **direction** (increase/ decrease), and **intensity** and/or **magnitude** of change.
- In addition to these standard measures, **focal-animal responses** were examined on **three different levels of complexity** by asking different key questions which related to **consistency** (How many penguins do respond?), **magnitude** (How much do they respond?), and **structure** (In what way do they respond?) of changes. The last level considered changes in 'syntax' (distribution of phase durations) and composition ('time budget') of both behaviour s.l. and heart rate.
- Following Objective No. 2, **focal-group evaluations** were performed in addition to the highly discriminative focal-animal evaluations[6] to test whether the necessary representativity with respect to 'penguin reality' was retained despite a higher degree of practicability[7] and greater approximation to observations effected by 'non-penguinologists'.

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[6] resulting in extensive transcription time (with respect to primary transcriptions alone: approx. total 1,750 h for behaviour s.l. and conspecifics; median per 30 min session: 13 h, per 45 min-session: 17 h)

[7] e.g., concerning primary transcriptions: reduction of time needed per session to an approximate median of 5 h, i.e., approximate total time = 150 h

- The dual objective of THIS STUDY resulted in an **'intertwined network' of analytical aspects**:
  - two 'resolution levels': Focal Animal & Focal Group
  - two indicator types: penguin behaviour s.l. & heart rate (dependent 'variables')
  - four types of disturbance: human, conspecific, predator, aircraft (independent 'variables')
  - four visiting regimes (with seven visiting stages plus pre- and post-visitation periods)
  - three visiting periods plus 'baseline'
  - three disturbance effects: immediate response during stimulus presentation, waning/ continuation post-withdrawal of stimulus, recovery
  - four response characteristics: prevalence, direction, intensity, and/or magnitude of change
  - three levels of complexity: consistency, magnitude, structure ('syntax' and composition).

- Consequently, data on penguin behaviour s.l. and heart rate were subjected to **five distinct sets of analyses**, each emphasising different aspects (and hence fine-grained to a different degree) with respect to independent and dependent parameters as well as analytical methods.

  A variety of **sampling and recording methods** was employed in combination, ranging from Instantaneous-Scan Sampling to Continuous Recording and Ad libitum to All-Occurrences Sampling. **Statistical procedures** comprised descriptive statistics and non-parametric tests; e.g., Friedman-test, Spearman's (partial) rank correlations.

  To gauge changes in intensity of different disturbance types (humans, conspecifics) in the course of a session, **Performance Indicator Values** were developed. Human disturbance was classified according to conduct, number, distance and duration of exposure of FA; for conspecific disturbance, type of interaction with FA, velocity of movement, number, and duration of exposure of FA were integrated. Due to rarity of occurrence, predator and aircraft disturbance was sampled ad lib. and assessed qualitatively.

1. Analyses of **focal-group behaviour aspects** (6 datasets; 30 s sampling units) focused on <u>applicability for untrained observers</u>: Six broadly categorised behaviour states, one behaviour event (headshakes), and posture were evaluated using <u>Instantaneous-Scan Sampling</u> (states, posture) and <u>All-Occurrences Sampling</u> (headshakes). Measurements of human visitation integrated distance, conduct and number, while conspecific total presence was used as a crude approximation to conspecific disturbance towards an entire group.
2. Analyses of **focal-animal behaviour elements and heart rate** focused on the <u>'disturbees'</u> by evaluating disturbance types within the timeframe chosen for focal animals. During transcriptions, behaviour was assigned to 31 different categories, complemented by posture and heart rate. <u>Second-by-second transcriptions</u> of behaviour/ posture were analysed as rates and/or durations per 20 s-interval, while heart rate was counted for 20 s and values were extrapolated to beats-per-minute (bpm-) values. Measurements of human visitation integrated distance, conduct and number, while conspecific presence and action was categorised according to distance from FA, velocity of movement and various types of interactions with FA.
3. Last, but not least, analyses of **focal-animal topography** focused on the <u>'disturbers'</u>, evaluating behaviour s.l. and heart rate within disturbance timeframes. Focal-animal topography visualised the poly-dimensional 'landscape' of animal behaviour s.l. and heart rate. <u>Second-by-second transcriptions</u> of behaviour s.l. yielded simultaneous information on behaviour (5 behaviour systems, comprising 31 behaviour elements) and posture (two categories) for each data point. They were complemented by 20 s-counts of heart rate (i.e., not extrapolated). Human visitation was depicted according to visiting stage, while conspecific movement, number, and distance were taken into account. Focal-animal topography was examined on <u>three response levels</u>:

a) **Focal-animal visual appraisal** offered the unique opportunity to examine <u>changes in overall comportment</u> (comprising behaviour s.l. and heart rate) as well as for 'isolated parameters'.

Qualitative visual appraisal was complemented by quantification of response consistency across focal animals. (Key question: How many?)

b) **Focal-animal quantitative comparison** quantified the magnitude of between-period changes in prevalence of behaviour and posture parameters as well as in heart rate variation. Additionally, variation of heart rate obtained during 'visited' sessions was compared to that recorded during 'baseline' sessions (no exposure to humans). (Key question: How much?)

c) **Focal-animal distribution of phases and states** examined the structure of comportment ('syntax', composition) by quantifying between-period changes in duration and number of phases for each comportment parameter. (Key question: In what way?)

On each of these levels, overall response to visitation as well as responses to visiting regimes differing in number and conduct of humans were evaluated.

- Due to their different foci, these sets of analyses contributed differently to each of the **seven aims** of this study (I-V = scientific aims, VI-VII = applied aims).

  Aim I: Quantification of Impact of Visitation on Behaviour s.l.
  Aim II: Quantification of Impact of Visitation on Heart Rate
  Aim III: Quantification of Extent of Individuality (Coping Strategies)
  Aim IV: Comparison of Impact of Human vs. Conspecific Disturbance
  Aim V: Quantification of Impact of Visiting Regimes
  Aim VI: Identification of Indicative Behaviours
  Aim VII: Identification of Threshold Distances

- In general, direction of responses obtained tallied well with **literature reports**, while disparities with respect to magnitude and/or intensity of response are suggested to derive from differences in species/ population (evolutionary history) and experimental/ study design on the one hand, and differential perception of the stimulus presented on the other.

- **Aim I: Impact of Visitation on Behaviour s.l.**

  Human visitation elicited **substantial changes** in incubating Adélie penguins' behaviour and to a lesser extent posture, both during the visit itself and after visitation. Alterations were still detectable **up until the fourth row**[8] into the colony; they concerned consistency (numbers of penguins responding), magnitude (decreases/ increases in prevalence of behaviours/ postures), the overall composition of behaviour/ distribution of the two postures, as well as changes in the 'syntax' of behaviour s.l. Differences between periods (pre, during, and after visitation) were most easily discernible for predominant behaviours, particularly those susceptible to social facilitation (i.e. rest, vigilance), but could be detected in **all parameters** examined.

- **Aim II: Impact of Visitation on Heart Rate**

  While positive correlations between extent of human disturbance and bpm-values of focal-animal heart rate were significant for only 8 of 12 focal birds examined, focal-animal topography demonstrated human visitation to likewise elicit **substantial changes**, both during the visit itself and after visitation. Alterations concerned consistency (numbers of penguins exhibiting increased heart rate), the overall composition of heart rate (distribution of phases among the categories below, within, and above mean resting heart rate ±2 SD) and the structure of heart rate ('syntax'). **Moving stimuli** generally elicited a stronger heart rate response than still ones irrespective of direction of movement (crouching down vs. getting up, retreat vs. approach). **Fluctuations in 'baseline' heart** rate examined in successive 10 min-intervals of 'baseline' sessions (i.e. without human visitation) were distinctly **less pronounced** with respect to increases in a number of descriptive statistical parameters as well as extent of variation in heart rate.

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[8] THIS STUDY did not look any further.

When comparing heart rate changes during disturbance (tachycardia) to those observed during **voluntary physical exertion** (diving: bradycardia), the stimulus trait ‘novelty’ (including ‘unpredictability’ and ‘uncontrollability’) is assumed to attain the greatest relevance.

To some extent, **heart rate and behaviour responses** appeared to be complementary, and at least for some birds observed, heart rate reactions might have constituted a precursor (‘surprise’/ ‘shock’/ ‘becoming aware’) to behaviour responses (‘taking overt action’ = coping).

- **Aim III: Extent of Individuality (Coping Strategies)**

  Considerable inter- and intra-individual differences were observed in the penguins studied, both outside and during human visitation. While some **inter-individual** differences in response **levels** (intensity, propensity to respond) seemed likely to be influenced by differential severity of visiting regime (s. Aim V), response **‘preferences’** (behaviour vs. heart rate; different behaviour systems) could not be attributed to visiting regimes or daily weather conditions, but might have been effected by micro-site (nest location within colony, e.g., inter-nest distances), age/ breeding experience, differential perception of stimulus (‘novelty’), or personality/ character/ temperament. Findings suggest **intra-individual** differences to reflect **‘general state of being’** prior to visitation, which is thought likely to be influenced by behaviour predominantly engaged in, and/or differential pre-visit exposure to predatorial or conspecific disturbance stimuli, and which was found to modulate behaviour responses during as well as after visitation.

- **Aim IV: Impact of Human vs. Conspecific Disturbance**

  Impact of human visitation was found to generally exceed that of conspecific presence and/or action: A greater intensity/ magnitude of responses was observed during human visitation, and this type of disturbance affected more comportment (behaviour s.l. and heart rate) parameters, indicating a **more profound disruption of comportment during human visitation**.

  For behaviours susceptible to both types of disturbance, a number of penguins displayed a **similar gradation** (decreased resting and increased vigilance at a greater distance, increased agonistics close up), but response changes occurred at substantially **greater distances for humans** than for conspecifics. Perhaps related to different minimum distances (humans: 3 m, conspecifics: at the focal nest), agonistic behaviours towards humans were not as commonly found as during conspecific interactions. A consistent response in **heart rate** was exclusively observed during human visitation. (Antarctic) **penguin evolutionary history** suggests that changes in intensity of behaviours displayed rather than ‘novel’ behaviours are to be expected when birds are subjected to a different (i.e., ‘evolutionarily novel’) type of disturbance stimulus (humans as predation-free predators). In this context, the farther-reaching disturbance response obtained during human visitation (i.e., changes in comportment parameters which were unaffected by ‘natural disturbers’, viz., conspecifics) might indicate that display of evolved behaviour in response to conspecific disturbance is experienced as ‘insufficient’ with respect to coping. Additionally, changes in structure and overall composition of comportment were found during human visitation, and these are proposed as a challenging but worthwhile **future field of investigation** when examining differences between conspecific and human disturbance.

  THIS STUDY found little evidence of a complementary relation between human and conspecific disturbance. Human visitation should thus be viewed as an as an **additional rather than an alternative source of disturbance**.

- **Aim V: Impact of Visiting Regimes**

  The regime differences hypothesised were **detectable on all levels** (How many?, How much?, In what way?) of focal-animal comportment examined, but discriminatory capacity varied between the levels. While the **most and least severe regimes** (3 P, L&F vs. 1 P, S&S) were **identified on all levels**, capacity to distinguish between the **entire gradation order** appeared to be at least partially dependent on sampling method (ISS every 30 s vs. second-by-second transcription), but might – to a lesser extent – also relate to individuals sampled (rows 1 to 4 for focal groups vs. rows 1 and 2 for focal animals). Cross-testing visitor conduct (loud and fast vs.

silent and slow) and number (1 vs. 3) generally suggested a **greater influence of conduct than number**, but did not permit extrapolation with respect to larger groups of visitors.

The idea of a closer approach being less harmful if the visitor keeps low should not be favoured over remaining at a larger distance in the first place: Crouching as well as getting up, approach as well as retreat was found to cause heart rate to peak and behaviour responses to increase.

Results obtained suggest **'selective decoupling' upon cessation of stimuli**, with a longer impact of conduct than number.

Apart from visitor conduct and number, penguin responses are suggested to be also influenced by **additional factors** such as duration of exposure or tightness of visiting group, all of which will interact with stimulus perception, which in turn is likely to be additionally mediated to an as yet unquantified extent by the valence attributed to various **stimulus traits**. The stimulus of human visitation is **multi-facetted** and its variability increases with number of people present, **true habituation** of penguins to anything but 'severely choreographed' human contact therefore seems unlikely.

- **Aim VI: Indicative Behaviours**

  Identification and classification of behaviours as indicative depends on **sampling methods** and **observer focus** (individuals, groups). A number of **penguin-inherent factors** (e.g., stage of breeding cycle, body condition, coping strategies, stimulus perception) as well as **time of day** have to be taken into account.

  In **penguin groups**, easily (i.e. for the 'untrained eye') identifiable indicative behaviours were found to be limited to those strongly influenced by social facilitation, i.e., increased vigilance and decreased resting, whereas examination of individual **focal animals** indicated all comportment parameters analysed to be affected by human visitation. On the group level, impact on these behaviours was obscured by different individuals changing different behaviours at different stages of the visit or in different directions (s. Aim VII), and choice of response behaviour was to some extent dependent on pre-visit behaviour displayed. Incorporation of these findings into **guidelines for visitor conduct** might be effected if people were advised to be additionally attentive to increased switches between behaviours of individual penguins (within-subject 'scattering'), and to increased incoherence of comportment displayed by different penguins (between-subject 'scattering').

- **Aim VII: Threshold Distances**

  Until quite recently, a **generic terrestrial threshold distance of 5 m** has represented the standard advice as regards all Antarctic birds. Nowadays, this distance is unanimously recognised as an oversimplification, and specifications pertaining to, e.g., species, stage of breeding cycle, and colony location have been proposed for a number of sites.

  Threshold distances are 'easy' to teach and to remember, and thus come in very handy for conservation education issues as well as tourism. The comportment parameters employed in THIS STUDY showed differences concerning the distance at which a) initial onset of marked responses and b) maximum responses were observed. Comparison of response distances across studies identified **three main problems** as regards the **concept of threshold distances**:

  1. Any generic threshold distance **lacks specificity**. With respect to Antarctic tourism, this error has to some extent been addressed by distribution of site-specific guidelines which include species- and breeding-cycle-specific threshold distances, but can of course not cater for individual differences pertaining to, e.g., state of nourishment, character/ personality/ temperament, or individual stimulus perception.
  2. Threshold distances constitute a **compromise between conservation and human interest**. This raises the question of appropriateness of distance determined ('Who is it for?') i.e., of acceptable **criteria/ cut-off points**. Heightened vigilance and decreased rest occurred as early as during visitor approach to 15 m in more than half of the sessions examined in THIS STUDY.

3. Threshold distances **do not take into account constraints in response repertoire**. Incubating penguins are 'tied' to their nests and thus subjected to motivational conflict ('flee and expose nest contents to predators/ climatic conditions' vs. 'stay and endure') which is likely to compromise their ability to cope.

- **Conclusions**
  - Impacts acting on Adélie penguins in the Antarctic Peninsula region are interwoven and jointly influence their welfare (as well as their fitness). While 'additivity' may be assumed, the **'whole disturbance'** is quite probably more than the sum of its components. With **global change** constituting an extra threat, human impact needs to be reduced, as human disturbance comes on top of everything else (e.g., for the colony investigated: conspecific disturbance, predator pressure, climatic change).
  - Adélie penguins do not exhibit human-specific behaviour. They show substantial inter- and intra-individual variability. Both findings lead to considerable **limitations** as regards **easily applicable and teachable (!) methods** for gauging impact.
  - The **critical distance** (>15 m) **for incubating Adélie penguins** found in this study was obtained by detailed behaviour observations and supported by heart rate recordings. While substantially greater than the currently advocated threshold distance (10 m, e.g., UBA 2009), it corresponded well with responses observed in freely moving penguins encountered outside the colony. Fortunately, the incubating penguins' responses at that distance included the parameters 'vigilance' (increase) and 'rest' (decrease). As these behaviours are most easily recognisable, an **increase of threshold distance to a minimum of 15 m** is proposed to be **warranted and feasible** and would improve the welfare of incubating Adélie penguins.
  - To heighten sensitivity to differences in stimulus perception among penguin individuals, **guidelines for visitor conduct** should advise people to be additionally attentive (i.e., while not losing sight of vigilance levels!) to increased switches between behaviours of individual penguins, and to increased incoherence of comportment displayed by different penguins, and to further extend human-penguin distance if these are observed. Furthermore, absence of agonistic behaviours should not be considered an indicator of 'unruffledness', whereas presence of these behaviours definitely indicates disturbance.
  - To **increase awareness** of welfare-conscious visitors as regards their potential impact, a **change in terminology** is suggested: The term penguin-mediated threshold distances characterises the distance to visitors chosen by those birds free to move away (currently not incubating). The term minimum tolerance-distance, in contrast, ought to be employed with respect to incubating birds for which response repertoire to (and hence controllability of) disturbance stimuli is seriously curtailed.
  - As results obtained on Adélie penguins breeding in a specific location cannot be extrapolated to other species/ locations, unequivocal recognition of the need for and subsequent adherence to empirically and scientifically confirmed **threshold distances that accommodate the various factors** (e.g., species, site, stage of breeding cycle, individual variation) should continue to be given high priority.
  - With respect to the considerably **shorter response distances** in (non-Adélie) penguins reported to be **'used' to human presence**, attribution to either habituation (penguins stopped caring) or to pre-study segregation (affected penguins already gone) appears to remain controversial, but an investigation of causality is suggested to be relevant as to the design of future management measures.
- **Prospects**
  - The **Modulation Model for Individual Response Differences** draws attention to the variety of levels on which behaviour observed at a given point (or period) in time is influenced prior to, during, and after stimulus presentation. FA-dependent response 'preferences' (comportment parameter), response intensities (measured as differential magnitudes of

response to ‘same’ stimulus), and response propensities (readiness to respond/ cease responding/ continue to respond), are suggested to merit further investigation, as these need to be incorporated in future models of response, if overall results are proposed to adequately reflect <u>focal-animal ‘reality’</u>.

- Currently, a number of penguin-inherent factors contributing to individuality are captured in <u>‘personality types’</u> which also serve to stress different coping strategies. Integration of environment-mediated intra-individual response ‘preferences’ (heart rate vs. behaviour, different behaviours) into such a typology might further our understanding of **response flexibility within a given ‘personality type’**.

7.2 Zusammenfassung

Die hier vorgestellte Untersuchung belegt qualitative und quantitative Verhaltens- und Herzfrequenzänderungen von brütenden Adéliepinguinen (*Pygoscelis adeliae*), die durch Menschen und/oder Artgenossen gestört wurden. Zusätzlich werden Beobachtungen bezüglich Störung durch Prädatoren und Fluglärm dargelegt.

- In den vergangenen zwei Jahrzehnten sah sich die antarktische Tierwelt insbesondere zwei belastenden Herausforderungen in zunehmendem Maße ausgesetzt, nämlich der globalen Klimaveränderung und der verstärkten Anwesenheit von Menschen (Tourismus, Freizeitaktivitäten des Stationspersonals und Wissenschaft). Um die Gesamtbelastung zu reduzieren, stellt das menschliche Verhalten gegenüber der antarktischen Tierwelt die einzige verbleibende Stellschraube dar, da es sehr unwahrscheinlich ist, daß sich die globale Klimaveränderung in absehbarer Zeit positiv beeinflussen läßt.

- Bei Antarktisbesuchern sind Mensch-Pinguin Begegnungen hoch geschätzt. Für die vorliegende Untersuchung wurden **Adéliepinguine** ausgewählt, da deren Verhaltensrepertoire sehr gut dokumentiert ist und diese Art zu den ‘ausdrucksstärksten’ unter den Pinguinen zählt. Außerdem werden Adéliepinguine gemäß der Roten Liste der IUCN als ‘least concern’ (Bestand nicht gefährdet) eingestuft, gelten aber gleichzeitig als ‘anfällig für menschliche Störung’.

  Für die Beobachtung wurden **brütende Pinguine** den ‘uneingeschränkt mobilen’ vorgezogen, weil Herzfrequenzmessungen bei den an das Nest gebundenen Vögeln weniger durch Bewegungsaktivität konfundiert sind (Untersuchungsplan), da die Pinguine dem menschlichen Besuch nicht ausweichen, um ihre Gelege/ Küken nicht zu gefährden. So sind sie menschlichen Einwirkungen ungeschützt ausgesetzt (Tierliche Befindlichkeit, gebräuchlicherer Fachterminus: Animal Welfare), während sie über nur begrenzte Möglichkeiten verfügen, aversive situative Einflüsse zu bewältigen (im Folgenden kurz als ‘Coping’ bezeichnet).

- Die vorliegende Arbeit folgte einer übergeordneten <u>dualen Zielsetzung</u>:
  1. Eine gründliche und umfassende **quantitative Analyse des Ausmaßes der Auswirkungen** menschlichen Besuchs wurde unternommen, um proximate Konsequenzen bzgl. Animal Welfare beurteilen und potentielle ultimate Folgen für die ‘fitness’ [sic] der Tiere einzuschätzen.
  2. Im Bestreben, einen Beitrag zur Entwicklung langfristig wirksamer Schutzkonzepte sowie zur **Erstellung ‘pinguinsensibler’ Richtlinien für menschliches Verhalten** zu leisten, wurden die Ergebnisse ‘hochauflösender’ (daher sehr arbeitsintensiver) Auswertungsprozesse mit solchen verglichen, die einen geringeren Zeitaufwand erforderten. Die Analysen wurden durch Überlegungen zur Umsetzbarkeit der Ergebnisse ergänzt.

- Die Durchführung der Besuchsexperimente im Freiland erfolgte in zwei aufeinanderfolgenden Jahren (2000, 2001), jeweils während der zweiten Hälfte der Brutperiode (Mitte/ Ende November bis Anfang Dezember). Die Freilanduntersuchungen fanden auf King George Island statt (= Isla 25 de Mayo, Süd-Shetland Inseln, maritime Antarktis). Die Datenerhebung für die vorliegende Arbeit wurde im SSSI 13[9] (jetzt ASPA[10] 132[11]) ‘in der Nähe’ der Argentinischen Station ‘Jubany’ vorgenommen; sie erfolgte im Anschluß an eine ‘Probefreilandsaison’ im SSSI 8 (jetzt ASPA 128[12]) in der Nähe der Polnischen Station ‘Henryk Arctowski’. An beiden Orten waren die Adéliepinguine keinen touristischen Besuchen unmittelbar in der Kolonie ausgesetzt.

- Insgesamt wurden **fünf Pinguingruppen** (mit 10 bis 48 brütenden Vögeln, Median = 22,5) sowie eine fluktuierende Anzahl aktuell nicht nest-gebundener Artgenossen untersucht. Aus diesen fünf Gruppen wurden insgesamt **23 Pinguine in Fokustieranalysen** einbezogen. Vier der fünf Gruppen wurden standardisierten Besuchsregimes ausgesetzt.

- Das Ausmaß der Störung wurde mit Hilfe von **ethologischen und physiologischen Parametern** beurteilt: Das **Pinguinverhalten** s.l. (‘abhängige Variable’; Verhalten und Körperhaltung, d.h. liegend oder sitzend/ stehend) wurde auf Video aufgezeichnet. Dieselben Bänder enthielten Informationen bzgl. Störung durch Artgenossen, Prädatoren und Fluglärm, während menschliche Störung sekundengenau protokolliert wurde (‘unabhängige Variablen’). Die **Herzfrequenz-messungen** erfolgten mit Hilfe künstlicher Eier, die mit einem Infrarotsensor ausgestattet in den Kieselsteinnestern der Pinguine ausgebracht wurden.

- Bei den einzelnen Aufzeichnungsereignissen (im Folgenden als ‘sessions’ bezeichnet) wurden die **Besuchs-’sessions’** (menschlicher Besuch findet statt) in **drei Perioden** – vor, während, nach – eingeteilt. Daneben wurden sogenannte **‘baseline sessions’** (besuchsfrei) aufgezeichnet. Die gesammelten Daten umfassen dementsprechend die Reaktionen von gänzlich ungestörten, ‘nur’ durch Artgenossen und/oder Prädatoren gestörten und von menschlichen Besuchen beeinflußten Pinguinen. Im Einklang mit der übergeordneten dualen Zielsetzung wurden die Informationen auf zwei Ebenen unterschiedlicher ‘Auflösungsstärke’ ausgewertet: **Fokusgruppenuntersuchungen (30 ‘sessions’)** wurden mit **Fokustieruntersuchungen (119 ‘sessions’)** kontrastiert.

- Die vorliegenden Ergebnisse basieren auf Daten von insgesamt
  - ca. **90** brütenden **Pinguinen**, von denen **23** zusätzlich als **Fokustiere** dienten
  - **47 h** (= 169.200 s) **Videoaufzeichnungen** (119 ‘sessions’)
  - **9.315 ‘Einheiten’** manuell ausgezählter **Herzfrequenz** (20 s-Intervalle aus 88 ‘sessions’)

- Gemäß der Zielsetzung 1 (s.o.) wurde ein **individuenbasierter, minimal-invasiver Forschungsansatz** gewählt. Während des Ausbringens der künstlichen Eier war jedoch ein gewisses Maß an ‘Eindringlichkeit’ unvermeidlich. Auf den dabei anwesenden Pinguinen angebrachte Farbmarkierungen ermöglichten eine nachfolgende Unterscheidung von ihren gänzlich unbeeinträchtigten Partnern und gewährleisteten damit ein Quantifizieren inter-individueller Unterschiede. Beobachtungen desselben Tiers an unterschiedlichen Tagen gaben Einblicke in intra-individuelle Unterschiede.

- Paarweise Vergleiche der drei Besuchsperioden (vor mit während, während mit nach, vor mit nach) sowie Vergleich jeder dieser Perioden mit ihrem Äquivalent in ‘sessions’ ohne menschliches Besuchsereignis (nur Herzfrequenz) wurden vorgenommen, um folgende Aspekte zu **quantifizieren**:
  a) **unmittelbares Störungsausmaß** während der Stimuluspräsentation (Vergleich während vs. vor dem Besuch)

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[9] SSSI = Site of Special Scientific Interest

[10] ASPA = Antarctic Specially Protected Area

[11] Potter Peninsula

[12] Admiralty Bay

b) **Persistenz/ Abklingen** der Reaktion nach Stimulusentzug (Vergleich während vs. nach dem Besuch)

c) Ausmaß der **Wiederherstellung des Vorbesuchszustandes** (Vergleich nach vs. vor dem Besuch)

d) spontane/ natürliche Schwankungen (‘baseline’)

Hierbei wurde der inter-individuell unterschiedlichen **Reaktionsbereitschaft** besondere Beachtung geschenkt. Verhaltens- und Herzfrequenzparameter wurden hinsichtlich ihrer **Prävalenz** (Prädominanz, Vorkommen, Abwesenheit), ihrer **Richtung** (Anstieg, Abfall) sowie ihrer **Intensität** und/oder ihres direkt gemessenen **Ausmaßes** der Veränderungen analysiert.

- Zusätzlich zu diesen Standardmessungen wurden **Fokustierreaktionen** im Hinblick auf verschiedene Schlüsselfragen auf **drei unterschiedlichen Komplexitätsniveaus** betrachtet. Diese bezogen sich auf **Konsistenz** (Wieviele Pinguine reagieren?), gemessenes **Ausmaß** (Wie stark reagieren sie?) sowie die **Struktur** der Veränderungen (Auf welche Art und Weise reagieren sie?). Das letzte Niveau berücksichtigte Veränderungen in der ‘Syntax’ (Verteilung unterschiedlicher Phasenlängen) und Komposition (‘Zeitbudget’) des Verhaltens s.l./ der Herzfrequenz.

- Gemäß Zielsetzung 2 wurden neben diesen hochauflösenden Fokustierauswertungen **Fokusgruppenauswertungen** vorgenommen, um zu untersuchen, ob die notwendige Repräsentativität bzgl. der ‘Pinguinrealität’ erhalten bleibt, wenn ein höherer Praktikabilitätsgrad und eine größere Ähnlichkeit mit durch ‘Nicht-Pinguinologen’ vorgenommenen Beobachtungen gewählt wird.

- Die o.g. duale Zielsetzung ergab ein **komplexes**[13] **Netzwerk analytischer Aspekte**:
  - zwei Auflösungsniveaus: Fokustiere und Fokusgruppen
  - zwei Indikatortypen: Verhalten s.l. und Herzrate (‘abhängige Variablen’)
  - vier Störungstypen: Menschen, Artgenossen, Prädatoren, Fluglärm (‘unabh. Variablen’)
  - vier Besuchsregimes (mit jeweils sieben Stadien sowie Vorher- und Nachher-Perioden)
  - drei Perioden pro Besuchs-’session’ sowie besuchsfreie ‘baseline sessions’
  - drei Störeffekte: unmittelbare Reaktion, Persistenz/ Abklang, Erholung
  - vier Reaktions-Charakteristika: Prävalenz, Richtung, Intensität u./o. Ausmaß der Veränderung
  - drei Komplexitätsniveaus: Konsistenz, Ausmaß, Struktur (‘Syntax’ und Komposition)

- Daher wurden die zu dem Pinguinverhalten s.l. und der Herzfrequenz aufgenommenen Daten **fünf verschiedenen Analysen** unterzogen, von denen jede, sowohl bzgl. der abhängigen und der unabhängigen Parameter als auch bzgl. der Analysemethoden, unterschiedliche Aspekte in den Vordergrund stellte.

  Die angewendeten **Sampling**[14]- (Wer und Wann?) und **Recording-Methoden** (Wie?) reichten von Scan Sampling (Betrachtung jedes Individuums der Fokusgruppe zu vorgegebenen Zeitpunkten) bis Continuous Recording (durchgängige, sekundengenaue Betrachtung des Verhaltens jedes einzelnen Fokustiers) und von Ad libitum zu All-Occurrences Sampling. Die **statistische** Auswertung beinhaltete deskriptive und analytische Methoden mit nicht-parametrischen Testverfahren, wie z.B. Friedman-Test und Spearman’s (Partielle) Rang-Korrelation.

  Um Intensitätsunterschiede der verschiedenen Störungstypen (Menschen, Artgenossen) abzuschätzen, wurden verschiedene **Kenngrößen** entwickelt. Menschliche Störung wurde hinsichtlich Verhalten, Anzahl, Entfernung und Zeitdauer der Einwirkung (auf das Fokustier)

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[13] engmaschig & knotenreich

[14] Die Begriffe Sampling- (Wer wird in welchen ‘Zeitfenstern’ untersucht?) und Recording-Methoden (Wie wird untersucht?) sind fester vokabulärer Bestandteil der deutschen Verhaltensforschung…

klassifiziert. Bei Artgenossen erfolgte eine ähnliche Einteilung: Sie berücksichtigte Art der Interaktion mit dem Fokustier, Bewegungsgeschwindigkeit, Anzahl und ‘Einwirkungsdauer’. Aufgrund ihres seltenen Vorkommens wurden Prädatoren und Fluglärm ad lib. aufgenommen und qualitativ abgeschätzt.

1. Bei den Analysen verschiedener **Verhaltensaspekte** von **Fokusgruppen** (6 Datensätze, 30 s Sampling-Einheiten) stand die Frage nach der Anwendungsmöglichkeit für ungeübte Beobachter im Vordergrund: Hierzu wurden sechs weiter gefaßte Verhaltenszustände (states), ein Verhaltensereignis (event; Kopfschütteln) sowie die Körperhaltung mit Hilfe von Scan Sampling (Zustände, Körperhaltung) und All-Occurrences Sampling (Kopfschütteln) ausgewertet. Die Kennzahl für das Ausmaß der Störung durch den menschlichen Besuch integrierte Entfernung, Besucherverhalten und -anzahl; bzgl. der Artgenossen wurde lediglich deren Anzahl als ‘grobe Approximation’ ihrer Störeinwirkung auf die Gesamtgruppe herangezogen.

2. In den Analysen der **Verhaltenselemente und Herzfrequenz von Fokustieren** war das Augenmerk auf die ‘Störungsempfänger’ gerichtet, indem der Störungstypus innerhalb des für die Fokustiere gewählten Zeitrahmens (20 s-Intervalle) ausgewertet wurde. Bei der Transkription wurde das Verhalten 31 verschiedenen Kategorien zugeordnet, daneben erfolgten Auswertungen der Körperhaltung (stehend/ sitzend, liegend) und der Herzfrequenz. Sekundengenaue Transkription von Verhaltenselementen und Körperhaltung ging als Anzahl und/oder Dauer pro 20 s-Intervall in die Analysen ein, während die Herzfrequenz pro 20 s-Intervall ausgezählt wurde und die ermittelten Werte als Minutenschlagfrequenz (bmp = beats per minute) analysiert wurden. Die Kennzahl für das Ausmaß der Störung durch den menschlichen Besuch integrierte Entfernung, Verhalten, und Anzahl der Besucher. In die Kennzahl für das Ausmaß der Störung durch Artgenossen flossen Anwesenheit, Entfernung vom Fokustier, Bewegungsgeschwindigkeit und verschiedene Interaktionsformen mit dem Fokustier ein.

3. Abschließend wurde für Analysen der **Topographie von Fokustierverhalten s.l. und Herzfrequenz** die Störquelle als Bezugspunkt gewählt, indem Verhalten s.l. und Herzfrequenz in dem durch die Störung vorgegebenen Zeitrahmen ausgewertet wurden. Die Fokustier-Topographie bildete die polydimensionale ‘Landschaft’ von Verhalten und Herzfrequenz ‘gesamteindrücklich’ ab. Sekundengenaue Transkription des Verhaltens s.l. lieferte Simultaninformationen bzgl. Verhalten (5 Verhaltenssysteme, bestehend aus den o.g. 31 Verhaltenselementen) und Körperhaltung für jeden Datenpunkt (jede Sekunde). Diese wurden durch Auszählung von o.g. 20 s-Intervallen ermittelte Herzfrequenzwerte ergänzt, die für diese Analysen nicht extrapoliert wurden. Das Ausmaß der menschlichen Störung wurde mittels der Besuchsstadien (Distanzen, Annäherung auf Distanz) dargestellt, während Entfernung, Anzahl und Bewegung von Artgenossen Berücksichtigung fanden. Die Fokustier-Topographie wurde auf drei Komplexitätsniveaus untersucht:

a) **Visuelle Einschätzung** ermöglichte es, Änderungen im Gesamtverhalten (einschließlich der Herzfrequenz) sowie in einzelnen Parametern unter die Lupe zu nehmen. Dieser qualitative Gesamteindruck wurde durch Quantifizierung beobachteter Antwortkonsistenzen über alle in die Analyse einbezogenen Fokustiere hinweg ergänzt. (Schlüsselfrage: Wie viele?)

b) **Quantitative Vergleiche** zwischen den Perioden (vor, während, nach) dienten der Ermittlung des Ausmaßes an Veränderungen in bezug auf Prävalenz der unterschiedlichen Verhaltenssysteme sowie der Variation in der Herzfrequenz. Zusätzlich wurde das Ausmaß der Variation in der Herzfrequenz zwischen Besuchs- und ‘baseline sessions’ verglichen. (Schlüsselfrage: Wie stark?)

c) Die **Analyse von Phasenverteilungen** untersuchte strukturelle Veränderungen im Gesamtverhalten (‘Syntax’, Komposition), indem Phasenverteilungsmuster (Phasenanzahl und -dauer) in den drei Perioden für jeden Parameter quantifiziert wurden. (Schlüsselfrage: Auf welche Art und Weise?)

Auf jedem dieser Niveaus wurde die Reaktion auf menschliche Besuche für alle Fokustiere zusammen sowie getrennt nach verschiedenen, sich in Anzahl und Verhalten der Besucher unterscheidenden Besuchsregimes ausgewertet.

- Gemäß ihren unterschiedlichen Schwerpunkten trugen die o.g. Analysen in verschiedenem Maße zu jedem der im Sinne der dualen Zielsetzung formulierten **sieben Ziele** bei (I-V: grundlagenforschungsbezogene Ziele, VI-VII: angewandte Forschungsziele).
  - Ziel I: Quantifizierung der Auswirkung menschlichen Besuchs auf das Verhalten s.l.
  - Ziel II: Quantifizierung der Auswirkung menschlichen Besuchs auf die Herzfrequenz
  - Ziel III: Quantifizierung des Ausmaßes der Individualität (Coping-Strategien)
  - Ziel IV: Vergleich: Auswirkung menschlichen Besuchs vs. Störung durch Artgenossen
  - Ziel V: Quantifizierung der Auswirkung unterschiedlicher Besuchsregimes
  - Ziel VI: Identifizierung von störungsanzeigendem Verhalten
  - Ziel VII: Identifizierung von störungsmindernden Schwellendistanzen

- Bezüglich der Reaktionsrichtung konnte insgesamt ein zufriedenstellendes Maß an Übereinstimmung der Ergebnisse aus der vorliegenden Arbeit mit **Literaturberichten** festgestellt werden. Es ist anzunehmen, daß die vorgefundenen Diskrepanzen im Hinblick auf Stärke/ Intensität der Reaktionen einerseits auf Art-/ Populationsunterschiede sowie Experiment-/ Studiendesign zurückzuführen sind; andererseits ist der individuell unterschiedlichen Wahrnehmung/ Bewertung des Reizes (menschlicher Besuch) verstärkt Bedeutung beizumessen.

- **Ziel I: Auswirkung menschlichen Besuchs auf das Verhalten s.l.**

  Menschlicher Besuch erzeugte **beträchtliche Veränderungen** im Verhalten von brütenden Adélie-pinguinen sowohl während des Besuchs als auch danach; in geringerem Maße wurde auch die Körperhaltung beeinflußt. Veränderungen ließen **sich bis einschließlich der vierten**[15] **Nesterreihe** der Kolonie feststellen, sie betrafen die Reaktionskonsistenz (Anzahl reagierender Pinguine), Reaktionsstärke (Änderungen in der Prävalenz von Verhalten/ Körperhaltung) und zeigten sich ebenfalls in Veränderungen bzgl. Komposition und ‘Syntax’ des Verhaltens s.l. Unterschiede zwischen den Perioden (vor, während, nach) waren am einfachsten in den prädominanten Verhaltensweisen auszumachen (Ruhe- und Aufmerksamkeitsverhalten), wurden aber in **allen untersuchten Parametern** gefunden.

- **Ziel II: Auswirkung menschlichen Besuchs auf die Herzfrequenz**

  Während eine positive Korrelation zwischen dem Ausmaß menschlicher Störung und Minutenschlagfrequenz nur bei 8 von 12 daraufhin untersuchten Fokustieren auftrat, ergab die Fokustier-Topographie Hinweise auf **deutliche Herzfrequenzveränderungen** während des Besuches und in der anschließenden Nachbesuchsperiode. Veränderungen betrafen die Reaktionskonsistenz (Anzahl reagierender Pinguine), Komposition (Verteilung der Herzfrequenz-Phasen auf die Kategorien ‘unterhalb’, ‘innerhalb’ und ‘oberhalb’ der mittleren Ruhefrequenz ±2 SD) und ‘Syntax’. **Bewegungsreize** erzeugten in der Regel stärkere Herzfrequenzreaktionen als unbeweglich dargebotene Stimuli (Mensch in bestimmter Distanz), unabhängig von der Bewegungsrichtung (in die Hocke vs. aus der knienden Position herauf; Annäherung vs. Rückzug). Was die Reaktionsstärke anging, fanden sich in aufeinanderfolgenden 10 min-Intervallen von **‘baseline-sessions’ deutlich schwächer ausgeprägte Herzfrequenz-Fluktuationen** als in Besuchs-’sessions’. Beim Vergleich von Herzfrequenzänderungen unter Störungseinfluß (Tachykardie, Steigerung) mit Veränderungen, die durch **freiwillige körperliche Anstrengung** bedingt waren (Tauchen: Bradykardie, Verlangsamung), wird angenommen, daß der Stimulusqualität ‘Neuheit’ die größte Relevanz zukommt.

  In gewissem Maße erschienen sich **Herzfrequenz- und Verhaltensantworten** zu ergänzen. Zumindest für einige Fokustiere könnten Herzfrequenzreaktionen eine Vorstufe (‘Überraschung’/

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[15] Nestreihen parallel zum Kolonierand; es wurden keine Daten über die vierte Reihe hinaus aufgenommen.

‘Schock’/ ‘Bewußtwerden’) zu nachfolgenden Verhaltensreaktionen (‘Reaktion im Sinne der Situationskontrolle’ = Coping) dargestellt haben.

- **Ziel III: Ausmaß der Individualität (Coping Strategien)**

  Deutliche inter- und intra-individuelle Unterschiede wurden bei den in dieser Arbeit untersuchten Pinguinen sowohl innerhalb als auch außerhalb des menschlichen Besuchs beobachtet. Während wahrscheinlich gemacht werden konnte, daß einige **der inter-individuellen** Unterschiede im **Reaktionsniveau** (Intensität, Antwortbereitschaft) durch unterschiedlichen Schweregrad der Besuchsregimes hervorgerufen wurden (s. Ziel V), konnten **Reaktionspräferenzen** (Verhalten vs. Herzfrequenz; verschiedene Verhaltenssysteme) weder mit Regime- noch mit wechselnden klimatischen Bedingungen in Einklang gebracht werden; als mögliche Einflußgrößen werden der ‘Mikrostandort’ (Position des Nests innerhalb der Kolonie, z.B. Zwischennest-Abstände), Alter und Fortpflanzungserfahrung, unterschiedliche Bewertung des angebotenen Reizes (Neuheitsgrad) sowie Unterschiede bzgl. Persönlichkeit/ Charakter/ Temperament angesehen. Die Ergebnisse deuten darauf hin, daß **intra-individuelle** Unterschiede den **‘Gesamtzustand’** vor dem Besuch widerspiegeln. Bei diesem wird eine Beeinflussung durch vor dem Besuch prädominant gezeigtes Verhalten (Motivationsanker) und/oder durch unterschiedlich ausgeprägte vor-besuchliche Konfrontation mit Störung durch Artgenossen oder Prädatoren als wahrscheinlich angenommen. Diesem ‘Gesamtzustand’ schien eine ko-regulierende Rolle sowohl während des Besuches als auch in der Nachbesuchsperiode zuzukommen.

- **Ziel IV: Auswirkung menschlichen Besuchs vs. Störung durch Artgenossen**

  Die Auswirkung menschlichen Besuchs war in der Mehrzahl der Situationen schwerwiegender als die durch Anwesenheit und/oder Verhaltenshandlungen von Artgenossen hervorgerufene: Während menschlicher Besuche wurde eine größere <u>Intensität/ Reaktionsstärke</u> beobachtet; zusätzlich wurden durch diesen Störungstypus <u>mehr Gesamtverhaltensparameter</u> (einschließlich Herzfrequenz) beeinflußt, was auf eine **tiefgreifendere Störung des Gesamtverhaltens durch menschlichen Besuch** hinweist.

  In für beide Störungstypen anfälligen Verhaltensparametern wurde eine **ähnliche Abstufung** der Verhaltensantworten beobachtet (vermindertes Ruheverhalten und erhöhte Vigilanz in größerer Entfernung, gesteigertes agonistisches Verhalten in größerer Nähe), bei der jedoch Reaktionsveränderungen im Zuge **menschlicher Besuche** in bedeutend **größerer Entfernung** stattfanden. Agonistisches Verhalten wurde menschlichen Stressoren gegenüber nicht so durchgängig gezeigt wie in Interaktionen mit Artgenossen, was möglicherweise im Zusammenhang mit den unterschiedlichen Minimaldistanzen steht (Menschen: 3 m, Artgenossen: direkt am Fokustiernest). Eine konsistente **Herzfrequenzreaktion** wurde ausschließlich bei menschlichem Besuch beobachtet. Die **Evolution** der (antarktischen) Pinguine legt nahe, daß man Intensitätsänderungen in der Verhaltensreaktion, nicht jedoch das Auftreten ‘neuer’ Verhaltensweisen erwarten sollte, wenn diese Vögel einem neuen Störreiz ausgesetzt werden. Die während menschlicher Besuche zu verzeichnende tiefergreifende Reaktion (d.h., Änderungen im Gesamtverhalten betrafen auch durch Artgenossen unbeeinflußte Parameter) könnte in diesem Kontext darauf hindeuten, daß der Einsatz von Verhaltensreaktionen, die im (evolutiven) Zusammenhang mit Störung durch Artgenossen entwickelt wurden, als unzureichend hinsichtlich des Coping empfunden wurde. Über diesen Einbezug bisher nicht-störungsspezifischer Verhaltensweisen hinaus könnten die während menschlicher Besuche aufgetretenen Struktur- und Kompositionsveränderungen im Gesamtverhalten ein schwieriges, aber lohnendes **zukünftiges Forschungsgebiet** bei der Betrachtung von Unterschieden zwischen Reaktionen auf Störung durch Menschen und Artgenossen darstellen.

  Im Zuge der Untersuchung wurden nur sehr eingeschränkte Hinweise auf eine komplementäre Beziehung zwischen menschlicher und artgenossenvermittelter Störung gefunden. Menschlicher Besuch sollte daher als eine **zusätzliche (nicht alternative) Störquelle** angesehen werden.

- **Ziel V: Auswirkung unterschiedlicher Besuchsregimes**

  Die angenommenen Regimeunterschiede konnten **auf allen Niveaus** (Wie viele? Wie stark?, Auf welche Art und Weise?) festgestellt werden, auf denen das Fokustier-Gesamtverhalten untersucht wurde. Das Ausmaß der Unterscheidungssensibilität war jedoch auf den einzelnen Niveaus unterschiedlich. Die **am stärksten und am wenigsten auf die Pinguine einwirkend postulierten Regimes** (drei Personen, laut und schnell vs. eine Person, langsam und leise) wurden **auf allen Niveaus richtig identifiziert**; ein Erkennen der gesamten graduellen Abfolge legte zumindest teilweise eine Abhängigkeit von der gewählten Sampling-Methode nahe (Scan Sampling alle 30 s vs. sekundengenaue Verhaltensniederschrift im Continuous Recording). Ein weiterer – jedoch als geringer einzustufender – Einfluß mag auch den ‘Versuchspinguinen’ zukommen (Nester-Reihen 1-4 für Fokusgruppenuntersuchungen vs. Reihen 1-2 für Fokustieruntersuchungen). Die verschränkte Prüfung (vier bzgl. Verhalten und Anzahl unterschiedlich kombinierte Regimes) der Faktoren ‘Besucherverhalten’ (laut und schnell vs. langsam und leise) und ‘Besucheranzahl’ (1 vs. 3) deutete darauf hin, daß im allgemeinen das **Besucherverhalten einen größeren Einfluß** auf das Pinguingesamtverhalten hatte als die Besucheranzahl, wobei die vorliegende Untersuchung keine Hochrechnung auf größere Besuchergruppen zuläßt. Die Vorstellung, daß eine Annäherung auf geringere Distanzen weniger störend ist, wenn die Besuchsperson eine gebückte Haltung einnimmt, sollte einem Verbleiben auf größeren Distanzen keinesfalls vorgezogen werden, da Bücken und Wiederaufrichten, Annäherung und Rückzug jeweils verstärkte Verhaltensantworten und Herzfrequenzerhöhungen hervorriefen. Die in dieser Arbeit vorstellten Ergebnisse legen eine **selektive Entkopplung** der Faktoren bei Stimulusentzug nahe, bei denen das Besucherverhalten länger nachzuwirken scheint.

  Zusätzlich zu Verhalten und Anzahl der Besuchspersonen werden Pinguinreaktionen durch **weitere Faktoren**, wie Dauer der Stimuluspräsentation (Besuchslänge) oder Kohäsion der Besuchsgruppe beeinflußt. Jeder Einflußfaktor interagiert mit der individuellen Reizwahrnehmung, die wiederum in einem noch nicht quantifizierten Maße von der Wertigkeit (Valenz) abhängt, die den verschiedenen Reizqualitäten (z.B. Neuheit, Intensität) beigemessen wird. Der Stimulus ‘menschlicher Besuch’ sollte daher als extrem **facettenreich** angesehen werden und dieser Facettenreichtum steigt mit wachsender Anzahl anwesender Personen. Eine tatsächliche **Gewöhnung (Habituation)** der Pinguine an menschlichen Besuch erscheint daher höchst unwahrscheinlich.

- **Ziel VI: Identifizierung von störungsanzeigendem Verhalten**

  Es konnte gezeigt werden, daß Identifizierung und Klassifizierung von Verhaltensweisen als ‘störungsanzeigend’ sowohl von den gewählten **Sampling-Methoden** als auch vom **Fokus** (Individuen vs. Gruppen) der beobachtenden Person abhängt. Außerdem müssen eine Reihe von **pinguin-inhärenten Faktoren** (z.B. Stadium im Fortpflanzungszyklus, körperliche Verfassung, Coping-Strategien, Reizbewertung) sowie **Tageszeit** beachtet werden.

  In **Pinguingruppen** waren ‘einfach’ (auch für Ungeübte) zu erkennende störungsanzeigende Verhaltensweisen auf diejenigen beschränkt, die in hohem Maße durch Soziale Aktivierung/ Stimulation (social facilitation) beeinflußt wurden, d.h. <u>erhöhte Vigilanz</u> und <u>vermindertes Ruheverhalten</u>. Dahingegen zeigte die Untersuchung einzelner **Fokustiere**, daß menschlicher Besuch Veränderungen in allen untersuchten Parametern hervorrief. Auf dem Niveau der Fokusgruppen wurden diese Veränderungen dadurch maskiert, daß unterschiedliche Pinguine unterschiedliche Verhaltensweisen in unterschiedlichen Stadien des Besuchs oder in unterschiedlicher Richtung änderten (s. Ziel VII) und die gewählte Verhaltensantwort zum Teil vom vor-besuchlich gezeigten Verhalten abhing. Diese Ergebnisse könnten einen Eingang in **Richtlinien für Besucherverhalten** finden, wenn Besuchspersonen den Rat erhielten, ihre Aufmerksamkeit zusätzlich – d.h., bei Nichtvernachlässigung des von den Pinguinen gezeigten Vigilanzverhaltens – sowohl auf <u>erhöhte Wechselfrequenzen</u> zwischen verschiedenen Verhaltensweisen von Individuen (‘intra-pinguinale Verhaltensstreuung’) zu richten, als auch auf eine <u>verstärkte Inkohärenz</u> im von unterschiedlichen Pinguinen gezeigten Verhalten s.l. zu achten (‘inter-pinguinale Verhaltensstreuung’).

- **Ziel VII: Identifizierung von störungsmindernden Schwellendistanzen**

  Vor gar nicht allzu langer Zeit galt das Einhalten einer **generischen 5 m-Schwellendistanz** als hinreichend für alle antarktischen Vogelarten. Heutzutage wird diese Distanz einhellig als zu grobe Vereinfachung angesehen, und für eine wachsende Anzahl von Gebieten wurden mittlerweile Spezifizierungen bzgl. Art, Stadium im Fortpflanzungszyklus und Lage der Kolonie vorgelegt.

  Schwellendistanzen sind leicht zu vermitteln und einfach zu lernen und kommen so der Naturschutzbildung und dem Tourismus sehr gelegen. Die in der vorliegenden Arbeit untersuchten Gesamtverhaltens-Parameter wiesen Unterschiede bzgl. der Distanz auf, bei der sie a) zum ersten Mal verstärkt auftraten und b) ihre maximale Veränderung erfuhren. Ein Vergleich der in unterschiedlichen Untersuchungen festgestellten Schwellendistanzen konnte **drei Hauptprobleme** herausarbeiten, die das **Schwellendistanzen zugrundeliegende Konzept** betreffen:

  1. Jedweder generischen Schwellendistanz **mangelt es an 'Treffsicherheit'**. Den antarktischen Tourismus betreffend [sic] ist diesem Problem mit der Erarbeitung und nachfolgenden Verteilung (z.B. auf Kreuzfahrtschiffen) lokalitätsspezifischer Richtlinien in gewissem Rahmen begegnet worden. Diese Richtlinien beinhalten z.B. art- und fortpflanzungszyklus-spezifische Schwellendistanzen, können aber selbstverständlich keine individuellen Unterschiede einbeziehen, die u.a. aus verschiedener körperlicher Verfassung, Charakter/ Persönlichkeit/ Temperament oder individueller Reizbewertung erwachsen.
  2. Schwellendistanzen stellen einen **Kompromiß zwischen Naturschutzbelangen und menschlicher Bedürfnislage** dar. Dieser Sachverhalt wirft die Frage nach der Angemessenheit der festgelegten Abstände auf (Auf wessen Bedürfnisse zugeschnitten?), d.h. nach akzeptablen **Kriterien der Distanzermittlung**. Erhöhte Aufmerksamkeit und vermindertes Ruheverhalten wurden z.B. in der vorliegenden Untersuchung in mehr als der Hälfte der analysierten 'sessions' bereits bei Annäherung der Besuchsperson auf 15 m festgestellt – volle 5 m vor der (bereits im Vergleich zur ehemaligen generischen Distanz verdoppelten) heute propagierten Schwellendistanz von 10 m für brütende Pinguine.
  3. Schwellendistanzen **mißachten Einschränkungen im Verhaltensrepertoire**. Brütende Pinguine sind an ihre Nester gebunden und dementsprechend motivationalen Konflikten ausgesetzt ('Fliehen und damit die im Nest befindlichen Eier/ Küken Prädatoren und den Umweltbedingungen aussetzen' vs. 'Bleiben und Ertragen'), die ihre Coping-Fähigkeiten deutlich einschränken.

- **Schlußfolgerungen**
  - Die auf Adéliepinguine in der Region der Antarktischen Halbinsel einwirkenden Belastungen sind miteinander verflochten und beeinflussen insgesamt die Welfare der Pinguine (und ihre 'fitness'). Eine kumulative Wirkung ist anzunehmen, doch ist das **Gesamtstörungsausmaß** (die 'ganze Störung') höchstwahrscheinlich größer als die Summe ihrer Einzelteile. Da die **globale Klimaveränderung** eine in den letzten Jahren verstärkt hinzugekommene Bedrohung darstellt, müssen die Auswirkungen <u>direkter menschlicher Einwirkung</u> auf die Pinguine vermindert werden, weil diese als <u>Zusatzbelastung</u> zu denjenigen tritt, denen die Pinguine ohnehin schon ausgesetzt sind (z.B. für die Pinguine der vorgestellten Untersuchung: Störung durch Artgenossen, Prädatoren, Klimaerwärmung).
  - Adéliepinguine zeigen <u>kein menschenspezifisches Störungsverhalten</u>. Sie weisen <u>beträchtliche inter- und intra-individuelle Variabilität</u> im Gesamtverhalten (inkl. Herzfrequenz) auf. Diese beiden Ergebnisse führen zu deutlichen **Einschränkungen** bzgl. **einfach anzuwendender und zu vermittelnder Methoden** zur Beurteilung des Störungsausmaßes.
  - Die **'kritische Distanz' für brütende Adéliepinguine** (>15 m) wurde in der vorliegenden Studie durch detaillierte Verhaltensbeobachtungen ermittelt und wird durch Auswertungen zu Herzfrequenzänderungen gestützt. Sie ist erheblich größer als die derzeitig postulierte Schwellendistanz (10 m, z.B. Umweltbundesamt 2009); hingegen stimmt sie gut mit dem von Pinguinen bevorzugten Mensch-Pinguin-Abstand überein, wie Verhaltensreaktionen

  freibeweglicher Pinguine außerhalb der Kolonie belegten. Da die Verhaltensantworten der brütenden Pinguine in dieser Distanz verstärktes Aufmerksamkeits- und vermindertes Ruheverhalten einschlossen und diese Verhaltensweisen auch für ungeübte Besuchspersonen leicht zu erkennen sind, erscheint eine **Anhebung der Schwellendistanz auf ein Minimum von 15 m angemessen und durchführbar**; die Welfare brütender Adéliepinguine ließe sich dadurch verbessern.

  - **Richtlinien** für (korrektes) **Besucherverhalten** sollten die Betreffenden auffordern, ihre Aufmerksamkeit auf erhöhte Wechselfrequenzen zwischen verschiedenen Verhaltensweisen von Individuen und auf eine verstärkte Inkohärenz im von unterschiedlichen Pinguinen gezeigten Verhalten s.l. zu richten – ohne dabei den Indikator ‘gesteigerte Vigilanz’ zu vernachlässigen – und den Mensch-Pinguin-Abstand bei Beobachtung dieser Veränderungen weiter zu vergrößern. In bezug auf agonistisches Verhalten sollte dessen Abwesenheit nicht als ‘Gleichmut’ gewertet werden; ein Auftreten dieses Verhaltens ist hingegen als deutliches Anzeichen von Störung anzusehen.
  - Um das **Bewußtsein** Animal-Welfare-interessierter Besuchspersonen bezüglich ihrer potentiellen Störwirkung zu **schärfen**, wird ein **Terminologiewechsel** vorgeschlagen: Der Ausdruck ‘Pinguinvermittelte Schwellendistanz’ charakterisiert den Mensch-Pinguin Abstand, der von ‘freibeweglichen’ (nicht brütenden) Vögeln gewählt wird. Der Terminus ‘Kleinster noch tolerierter Abstand’ hingegen sollte für brütende Pinguine verwendet werden, deren Verhaltens-repertoire (und damit ein Spektrum an Kontrollmöglichkeiten) in bezug auf Störreize stark eingeschränkt ist.
  - Da die hier vorgelegten Ergebnisse von Adéliepinguinen einer bestimmten Kolonie stammen und somit nicht einfach auf andere Arten/ Örtlichkeiten übertragen werden können, sollte der Ermittlung und nachfolgenden Einhaltung empirisch und wissenschaftlich bestätigter **Schwellendistanzen, die die verschiedenen Einflußfaktoren berücksichtigen** (z.B. Art, Örtlichkeit, Stadium im Fortpflanzungszyklus, individuelle Variation) weiterhin hohe Priorität gewährt werden.
  - Eine Bewertung der deutlich **geringeren Schwellendistanzen** – wie sie von **‘an Menschen gewöhnten’** (nicht-Adélie) Pinguinen berichtet wird – als ‘Habituation’ (vorhandene Pinguine nicht länger gestört) oder ‘Segregation vor Untersuchungsbeginn’ (gestörte Pinguine nicht länger vorhanden) erscheint derzeit nicht abschließend möglich. Eine Untersuchung der Kausalzusammenhänge dürfte sich jedoch als relevant für die Ausgestaltung zukünftiger Management-Maßnahmen erweisen.

- **Ausblick**
  - Das **Modulations-Modell individueller Reaktionsunterschiede** lenkt den Blick auf die verschiedenen Niveaus, auf denen ein zu einem bestimmten Zeitpunkt/ einer bestimmten Zeitperiode beobachtetes Verhalten vor, während und nach der Reizpräsentation beeinflußt wird. Fokustierabhängige Antwortpräferenzen, Antwortintensitäten und Antwortbereitschaften sollten weiter erforscht werden, da diese in zukünftige Reaktions-Modelle integriert werden müßten, um die Realität der Fokustiere adäquat widerzuspiegeln.
  - Aktuell werden verschiedene pinguin-inhärente Faktoren, die zur Individualität beitragen, in ‘Persönlichkeitstypen’ gebündelt, die auch der Verdeutlichung unterschiedlicher Coping-Strategien dienen können. Die Integration umweltvermittelter intra-individueller Antwortpräferenzen (Herzfrequenz vs. Verhalten; verschiedene Verhaltensweisen) in eine solche ‘Typologie’ könnte vertiefte Einblicke in die **Reaktionsflexibilität innerhalb eines ‘Persönlichkeitstyps’** ermöglichen.

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"Penguins are beautiful, interesting, inspiring, and funny." (George Gaylord Simpson 1976, dust jacket to Penguins – Past and Present, Here and There)

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[1] A note for German readers: Original spelling has been left unchanged, e.g., behaviour (British English) vs. behavior (American English).

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Erklärung

Ich versichere, daß ich meine Dissertation **'Impact of Human and Other Disturbance on Behaviour and Heart Rate of Incubating Adélie Penguins (*Pygoscelis adeliae*)'** selbständig, ohne unerlaubte Hilfe angefertigt habe und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe. Alle vollständig oder sinngemäß übernommenen Zitate sind als solche gekennzeichnet. Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen in- oder ausländischen Hochschule anläßlich eines Promotionsgesuchs oder zu sonstigen Prüfungszwecken eingereicht.

Marburg, 22.11.2010 ____________________________

(Kathrin C. Schuster)