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Adaptations of the rare endemic Grey Falcon *Falco hypoleucos* that enable its permanent residence in the arid zone of Australia

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Abstract

The Grey Falcon *Falco hypoleucos* is an extremely rare and little known Australian endemic raptor. The Web of Science lists only two publications for this species, considered to be one of the five rarest *Falco* species of the world: a literature review and analysis of museum material (Olsen and Olsen 1986), and the results from the preliminary investigation that led to this study (Schoenjahn 2013). The difficulty in finding these rare birds (<1000 mature individuals), distributed thinly across much of Australia’s arid/semi arid zone (~5 million km^2), hampers detailed studies and has deterred previous researchers from studying this species.

The Grey Falcon is the only species of *Falco* to have its entire population confined exclusively to a hot arid environment. To understand the processes that help the species to persist in its extreme environment, I explore key aspects of its ecology, morphology, and anatomy, using observational data collected during 14 field seasons (2003–2016), involving 59 breeding events and satellite tracking data from seven individuals tracked for between 82 and 797 days.

How do individuals, during the various stages of their lives, cope with extremely high ambient temperatures? Investigating whether the species is specifically adapted behaviourally and anatomically to its environment, I found that Grey Falcons keep physical exertion and thus activity levels low in each aspect of their day-to-day lives, and lack particular morphological or physiological characteristics that would help them to cope with heat better than other bird species do. A possible explanation of the behaviour to keep activity levels low is that this helps to keep endogenous heat production low which enables these birds to respond to extreme and unexpected environmental changes without delay.

The breeding ecology of the Grey Falcon is characterized by a behaviour that is unique among birds of prey. The young often stay with their parents for up to 12 months or longer after fledging, i.e. well into the next breeding season, and some of these young were even fed by their parents at this advanced age. I show that this behaviour may be interpreted as a consequence of Grey Falcons of all ages keeping their activity levels low at all times.

The movements of individuals is a further key aspect in the ecology of a species, particularly so in desert-living birds. The Grey Falcon lives exclusively in an area where at least 45% of the regularly breeding bird species are considered to be nomadic. I found that the movement patterns of the Grey Falcon are generally nomadic, but are characterized by a distinct and unusual element of reluctance. That is, if conditions become inadequate for

breeding these birds rather stay and forego breeding than embark on a search for more favourable conditions that may be far away, and could expose them to risk. Although capable of long-distance movement (one individual moved more than about 1000 km in nine days), Grey Falcons appear to move on only when environmental conditions become a risk to their survival, i.e. only when absolutely necessary, and when they do move on, they move no farther than necessary. I term this behaviour ‘reluctant nomadism’.

An unexpected behaviour brought to light by this study is that Grey Falcons often roost on the bare ground at night. This behaviour was noted on 149 (26%) of 576 nights that Grey Falcons were recorded at locations other than the nest. They roosted on the ground at times even when trees (and their nest) were within view. I propose that this is also a consequence of the species’ behaviour of keeping activity levels low at all times. Night-roosting on the bare ground exposes these birds to predation by recently introduced cats, foxes, and dingoes. A further hitherto unrecognized threat to the species is suggested to be climate change. This threat derives from extreme climatic events that characterize the species’ environment, and is a consequence of the species’ behaviour to remain at all times in the arid/semi-arid zone. This hot environment is characterized by extreme and unpredictable climatic events, and these are predicted to increase in frequency, severity, and duration over time.

In summary, in key aspects of its ecology, the behaviour of the Grey Falcon shows markedly low levels of physical exertion. The consistency suggests that the species’ ecology is, consequently, governed by the principle of keeping physical exertion low. I interpret this behaviour as an adaptation of the species to its hot arid environment, one that is characterized by extreme and unpredictable climatic events. Keeping levels of physical exertion low helps to keep endogenous heat production low. This enables these birds to respond to adverse climatic events without delay even under challenging circumstance, thus enabling the Grey Falcon’s permanent residency in the hot arid and semi-arid zone of Australia.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, financial support and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my higher degree by research candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Conference abstracts

2016

Ecological Society of Australia Annual Conference ‘ESA16’, 28 Nov. – 2 Dec. 2016, Fremantle, Western Australia.

Presentation title:

‘Can climate explain the delayed juvenile independence and slow behavioural development in the Grey Falcon?’

2015

International Raptor Conference of the Raptor Research Foundation, 4–8 Nov. 2015, Sacramento CA, USA.

Presentation title:

‘Delayed independence in young of the desert-dwelling Grey Falcon (*Falco hypoleucos*) of Australia: a description and possible explanation of a unique behavior in raptors.’

Publications included in this thesis

No publications included.

Contributions by others to the thesis

Gimme Walter and Chris Pavey contributed to this thesis in critically revising it so as to contribute to the interpretation. David Booth commented critically on early drafts.

Statement of parts of the thesis submitted to qualify for the award of another degree

None.

Research involving human or animal subjects

The study required animal ethics approval. The following overview summarizes the approvals for the states and territories involved, covering the fieldwork period of the PhD-programme (15/09/2014 to 15/09/2017). For the full names of the committees see the respective document.

State/Territ.	Agency	Approving Committee	Reference number	Start date	End date	Appendix #
NSW	DPI	DG's ACEC	10/1354	22/03/2013	22/03/2016	6A
	DPI	DG's ACEC	16/350	22/03/2016	22/03/2019	6B
NT	CDU	AEC of CDU	A12018	16/04/2014	16/04/2016	6C
	CDU	AEC of CDU	A12018	30/03/2016	30/03/2020	6D
Qld	UQ	NEWMA AEC	SBS/308/14	15/09/2017	15/09/2017	6E
	DAFF	DAFF AEC	CA 2013/04/684	01/07/2013	30/06/2016	6F
	DAF	DAF AEC	CA 2016/04/955	01/07/2016	07/04/2019	6G
SA	DEWNR	WEC	14/2013	01/07/2013	30/06/2016	6H
	DEWNR	WEC	13/2016	26/05/2016	26/05/2019	6I

Key to the abbreviations of the agencies' names:

CDU	Charles Darwin University (NT)
DAF	Dept. of Agriculture and Fisheries (Qld)
DAFF	Dept. of Agriculture, Fisheries and Forestry (Qld)
DEWNR	Dept. of Environment, Water and Natural Resources (SA)
DPI	Dept. of Primary Industries (NSW)
UQ	The University of Queensland

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A study of such an elusive species spanning some 15 years while covering much of Australia's remotest areas is impossible without the help of very many people, and my heartfelt thanks go to all these wonderful people who supported me and this impossible study over the years. I hope that they will continue to do so. More than 400 persons kindly shared their sightings and photos with me, patiently answering further and further questions about the details of their observations; many breeding sites I discovered by *in situ*-investigations of such reports. Many people went out of their way to check likely and unlikely sites for me, often at remote locations, thus adding crucial information to the research data. Special thanks go to Lisa Nunn, Lisa even found a transmitter in the desert that one of 'my' birds had shed a few days earlier. For strengthening the manuscript I thank David Booth.

The study would have been impossible without access to many private properties and other land of restricted access, and my sincere thanks go to the persons kindly granting me such access, often at short notice or even on the spot. My sincere thanks go to those who supported this study in many other ways, be it by publicizing my requests for sightings on their websites, newsletters, or information boards, be it by helping with sourcing literature, facilitating contacts, and providing data held at research and governmental institutes, facilitating contacts, processing my permit and licence applications quickly when time was critical, and for mental support when it was most needed. I thank the team at the Banding Office (ABBBS), and David Drynan in particular for supplying colour-coated bands.

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Keywords

bird of prey, raptor, endotherm, extended juvenile dependence, movement, satellite telemetry, satellite tracking, reluctant nomadism, threatened species, conservation

Australian and New Zealand Standard Research Classifications (ANZSRC)

ANZSRC code: 060201, Behavioural Ecology, 40%
ANZSRC code: 060299, Ecology not elsewhere classified, 20%
ANZSRC code: 060303, Biological Adaptation, 40%

Fields of Research (FoR) Classification

FoR code: 0602, Ecology, 80%
FoR code: 0603, Evolutionary Biology, 20%

Frontispiece

The photos illustrate some of the species-specific behavioural and anatomical characteristics of Grey Falcon. The chapter relevant to each of these features is indicated.

(A) Grey Falcon, adult. The state of our knowledge on the species is outlined in **Chapter 1. Chapter 2** explores key behaviours and features of the plumage in relation to the hot arid environment inhabited by this species, and compares the results with those from other species of *Falco*.

(B) The unusual behaviour of members of a family staying together as a close group for extended periods after fledging of the young is explored in **Chapter 3**. The photo shows two members of a family of four, a juvenile female on the left and its male parent on the right. The photo was taken on 29 Apr., about 6 1/2 months after the presumed fledging date of that juvenile.

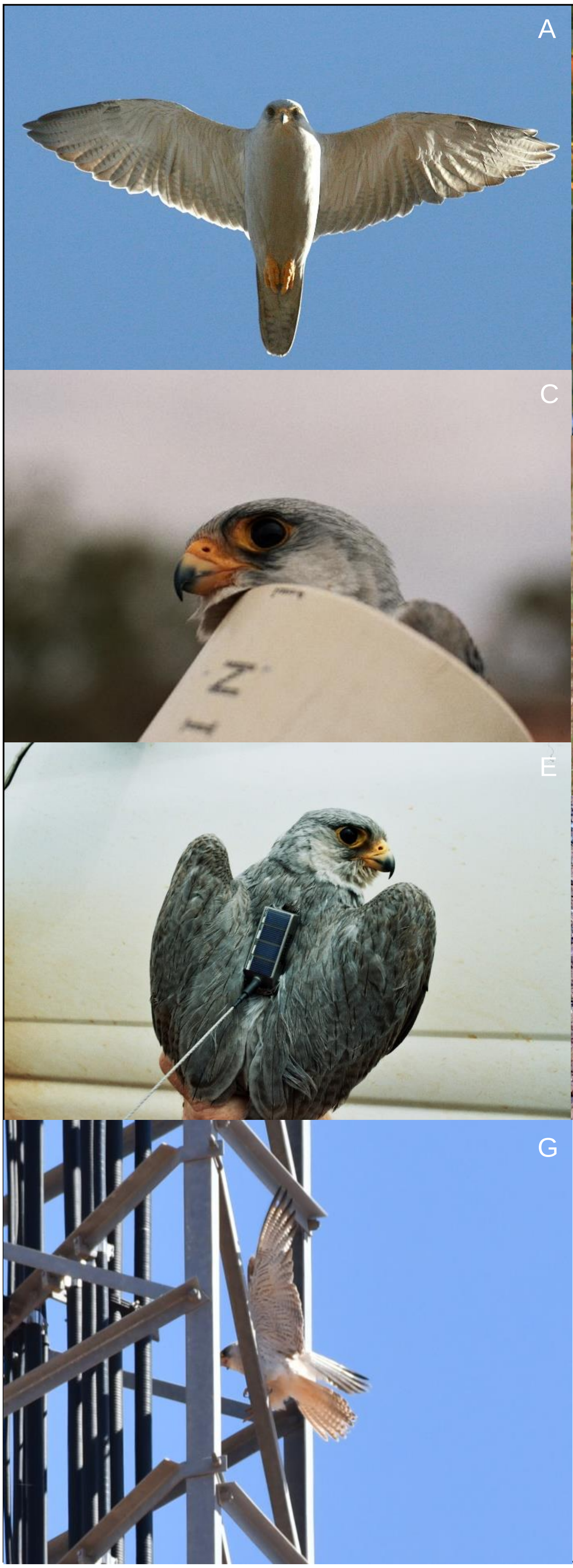
(C) Grey Falcon, adult male. Individuals were captured for colour-banding for future individual identification. Movements are explored in **Chapter 4**.

(D) Grey Falcon, adult female. During this study it was found that Grey Falcons often roost on the ground at night. This behaviour exposes these birds to predation by introduced carnivores (**Chapter 5**).

(E) Grey Falcon, adult male Argos ID 79109, with a solar-powered Doppler-shift satellite transmitter mounted as a backpack using a custom-made harness of Teflon® ribbon. These transmitters were used to monitor the long- and short-term movements of selected individuals (**Chapter 4**). This bird was satellite-tracked for 18 months and bred successfully twice during that period.

(F) Remains of the satellite-tagged adult male Argos ID 141276 (Qld). Circumstantial evidence suggests that this bird was killed and eaten by a feral cat while roosting on the ground at night (**Chapter 5**).

(G) A yearling Grey Falcon is landing clumsily on an angled bar in the lower section of a repeater tower, begging loudly while one parent roosts at the top of the same tower. Adult birds, by contrast, always land on horizontal bars and never on angled bars. The extremely delayed skill development and extended period of juvenile dependence in Grey Falcons is explored in **Chapter 3**.



For descriptions see opposite page.
Photo credits:

(A) Chris Field
(B) Allan Friis
(C) JS
(D) Gary Porter
(E) JS
(F) JS
(G) Marieke T. Mourik - de Goede & Vincent Mourik

Preface

During preliminary work on this project, between 1998 and 2003, I received predominantly discouraging feedback from other researchers that I had consulted. They considered a study on Grey Falcon simply unfeasible. This led to an increase of my endeavours, and from then on my credo was:

> *Wenn eine Idee am Anfang nicht absurd klingt, dann gibt es keine Hoffnung für sie.*
> *(If at first an idea does not sound absurd, then there is no hope for it.)*
> Albert Einstein (1879–1955).

After having collected some first data in the field and from museum holdings, I became aware that any data claimed to pertain to the species may not be genuine. I found that it had to be checked thoroughly. When I realised that John Gould's type specimen had later been misidentified, I made this my maxim:

> *Take nothing on its looks; take everything on evidence. There's no better rule.*
> *Charles Dickens, in "Great Expectations" (1860).*

Today, 15 years into this study and having driven almost the distance to the moon in search of Grey Falcons, I feel that I will continue to study this species beyond the completion of the PhD program, not with the same intensity perhaps, but for many years to come,

> *ist doch der Vogelkunde von jeher nicht nur mit dem Verstand, sondern auch mit dem Herzen gedient worden.*
> *(for ornithology has ever been served not only with the intellect, but also with the heart.)*
> *Erwin Stresemann, in "Die Entwicklung der Ornithologie von Aristoteles bis zur Gegenwart" (1951).*

Jonny Schoenjahn, Perth, February 2018.

For Stephanie

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List of abbreviations used in the thesis

AM	Australian Museum
IUCN	International Union for Conservation of Nature
LST	Local solar time
mya	Million years ago
NP	National Park
PNG	Papua New Guinea
PTT	Platform Transmitter Terminal, i.e. a Doppler satellite transmitter
TC	Tropical Cyclone

NSW	New South Wales
NT	Northern Territory
Qld	Queensland
SA	South Australia
WA	Western Australia

N., E., S., W.	Points of the compass. Also used are composites, e.g. NW, ESE.

Chapter 1

State of knowledge of the ecology of the Grey Falcon and justification for the research questions and methodology of this thesis

1.1 Aims, significance, and expected outcomes

The aim of this study is to explore the adaptations of the Grey Falcon *Falco hypoleucos* that enable its persistence at extremely low density in arid and semi-arid environments.

The Grey Falcon is an extremely rare and little known Australian endemic raptor. It persists at unusually low densities exclusively in the arid and semi-arid zones of Australia (Schoenjahn 2013), an environment that is characterised by unpredictable and extreme periods of boom and bust (Morton et al. 2011). The entire population of no other species of *Falco* persists exclusively in such an arid environment (Appendix 1). Despite this circumstance the Grey Falcon is not a food generalist but specialises on a single type of prey, namely birds within a particular size range (Schoenjahn 2013). From this, and the unpredictability of its arid environment, one may expect that the species is nomadic, because many bird species populate Australia's arid and semi-arid zones during boom periods and move out when the environment again becomes stark. However, published reports and assertions with regard to movements of Grey Falcons do not confirm unanimously that the species is nomadic.

Further, the species is extremely rare. Its estimated population size of less than 1000 individuals (Schoenjahn 2011a) may be well below the general minimum census size accepted for populations to be genetically viable in perpetuity (Traill et al. 2010). Therefore, a decrease in the overall population size caused by locally increased mortality rates, as a result of temporarily adverse environmental conditions, for example, increases the risk of extinction for the species as a whole. Despite all these circumstances the Grey Falcon persists, with no evidence of a decline since the species became known to science in 1839 (Schoenjahn 2010a).

To understand the processes that help the species to survive in such extremely low numbers in its extreme environment, I explore in this thesis key aspects of the species' ecology, morphology, and anatomy, and identify whether these aspects are of significance with regard to the persistence of the species in its extreme environment. My findings also provide novel insights into the functioning of arid ecosystems that will benefit the management of these systems.

1.2 Synopsis of common elements in the ecology of raptors

The terms 'raptor' and 'bird of prey' are reserved customarily for the species that make up the orders Falconiformes (diurnal raptors, traditionally including the family Cathartidae) and Strigiformes (nocturnal raptors, i.e. owls) (Brown and Amadon 1989). The families within these two orders evolved from three or more ancestral lineages (Jarvis et al. 2014), a discovery that will undoubtedly affect their future higher classification. Most species in these two orders share a predatory disposition and carnivorous diet and have anatomical features, such as talons and a hooked beak, that enable them to hold prey and tear apart food (Snyder and Snyder 1991). The distribution of raptors is virtually worldwide (e.g., Brown and Amadon 1989) and they are found in virtually all types of environments.

In body mass raptors range from the Collared Falconet *Microhierax caerulescens* (30–50 g) (White et al. 1994) to the Andean Condor *Vultur gryphus* (males up to 15 kg). With a wingspan of up to 320 cm the Andean Condor is among the largest of the extant flying birds (Brown and Amadon 1989, Houston 1994). Raptors are generally long-lived and have a low reproductive rate, larger species typically more so than smaller species (Newton 1979). Mortality rates are difficult to quantify, but it is well established that immature birds experience much higher mortality rates than adults, and smaller species higher rates than larger species (Newton 1979, Newton et al. 2016). Raptor species may be solitary or colonial when they breed and they often nest in the same general area year after year (Newton 1979). With regard to movements, Newton (1979, p. 201) noted that observed patterns may often be explicable by changes in food supply. For example, many species leave their northern hemisphere breeding grounds and migrate south before food becomes too scarce or difficult to obtain during the boreal winter (Lack 1968, Berthold 1996).

1.3 Grey Falcon ecology and origin

Our knowledge of the Grey Falcon is limited. A search of the Web of Science (http://apps.webofknowledge.com/, using the terms 'Grey Falcon' and 'Falco hypoleucos', verified 1 Mar. 2016) returned only two publications for this species for the period 1900–2015. They include a literature review by Olsen and Olsen (1986), which also contains an analysis of data obtained from materials held in specimen collections, and a research paper by Schoenjahn (2013) that contains results from the preliminary investigation that led to this study. This paucity of peer-reviewed scientific literature indicates that the knowledge base on Grey Falcon derives from anecdotal and secondhand reports. The reason for such scant reporting on these birds is the difficulty of collecting data from a species distributed in extremely low numbers over a vast area that is remote, frequently inaccessible and often hazardous (Schoenjahn 2013). A comprehensive summary of what was known about the species up to the early 1990s is provided in the *Handbook of Australian, New Zealand and Antarctic Birds,* Vol. 2, edited by Marchant and Higgins (1993). A summary of information available as at July 2014, when the research for this thesis was begun, makes up the remainder of this section. Later publications on Grey Falcon largely confirm the state of knowledge of 2014. Note that most information is in sources not covered by the Web of Science.

Population size, and body mass

The Grey Falcon is an elusive species endemic to mainland Australia where it is the rarest of six members of the genus *Falco* that are found there (Olsen and Olsen 1986, Marchant and Higgins 1993). The species consists of a single population and is considered monotypic (Marchant and Higgins 1993). The total population size is now generally accepted to be <1000 mature individuals (Schoenjahn 2011a, Garnett et al. 2011, BirdLife International 2012). This is considerably less than what was accepted earlier (up to 5000 individuals) (Brouwer and Garnett 1990, Garnett and Crowley 2000), making the species one of the five rarest *Falco* species in the world (Schoenjahn 2013).

The Grey Falcon is a medium-sized raptor, with males weighing on average just below 400 grams and females slightly above 500 grams (Schoenjahn 2011b). Hence, like all approximately 38 species in that genus (del Hoyo and Collar 2014), the Grey Falcon exhibits reversed sexual dimorphism (RSD) in body mass, with females weighing on average about 30% more than males (Schoenjahn 2011b).

Distribution

The Grey Falcon is distributed sparsely over Australia's arid and semi-arid zone, an area of about 5 million km^2 (Australian Museum 2002, Pavey and Nano 2006). The species appears to be absent from Cape York Peninsula, areas east of the Great Dividing Range in Queensland and New South Wales (NSW), south of the Great Dividing Range in Victoria, and south of latitude 26ºS in Western Australia (Barrett et al. 2003). Occurrence records from these extralimital areas (many of which have previously been accepted, for example by Barrett et al. (2003)) are likely the result of misidentification because no indisputable records come from any of them (Schoenjahn 2013). For example, an individual shot by A. Clark on 10 Sep. 1895 at Bulga NSW, about 75 km inland from Newcastle on the Pacific coast, was claimed to be a Grey Falcon (North 1912). The specimen was presented to the Australian Museum (AM), its accession number is AM O.8339, but the specimen cannot now be found. The occurrence of the Grey Falcon thus cannot be confirmed from that locality. Further, at least some historical breeding records from those areas that were accepted as genuine by Olsen and Olsen (1986), are based almost certainly on misidentified clutches of eggs in museum collections (Schoenjahn 2013). The breeding distribution is confined to climate zones in Australia with the highest annual average temperatures (Figure 1.1), that is the arid and semi-arid zone.

Outside of these zones Grey Falcons have been recorded rarely and, typically, outside the core breeding season, and reports almost exclusively involve single individuals. For example, a single individual was photographed on 5 July 2007 at Pine Creek, Northern Territory (NT), i.e. north of the arid zone and about 340 km NNW of the northernmost breeding record verified by Schoenjahn (2013). Such verified records of Grey Falcons outside of the arid zone are rare.

Alleged records from Australian islands all concern islands close to the Queensland coast: Dunk Island (Banfield 1906, 1908, 1924, Tarr 1948, Austin 1950), Green Island (Olsen and Olsen 1986) (without providing a reference), and Fraser Island (Roubin 2005). However, those records pertain without doubt to birds of prey of other species (Olsen and Olsen 1986, Schoenjahn 2010b). Alleged records outside Australia come only from Papua New Guinea. However, those claims should be treated as unconfirmed, given the circumstances of the observations (Table 1.1). Indeed, none of the observers involved provided convincing descriptions of fieldmarks or behaviours, as described by Schoenjahn (2010b).

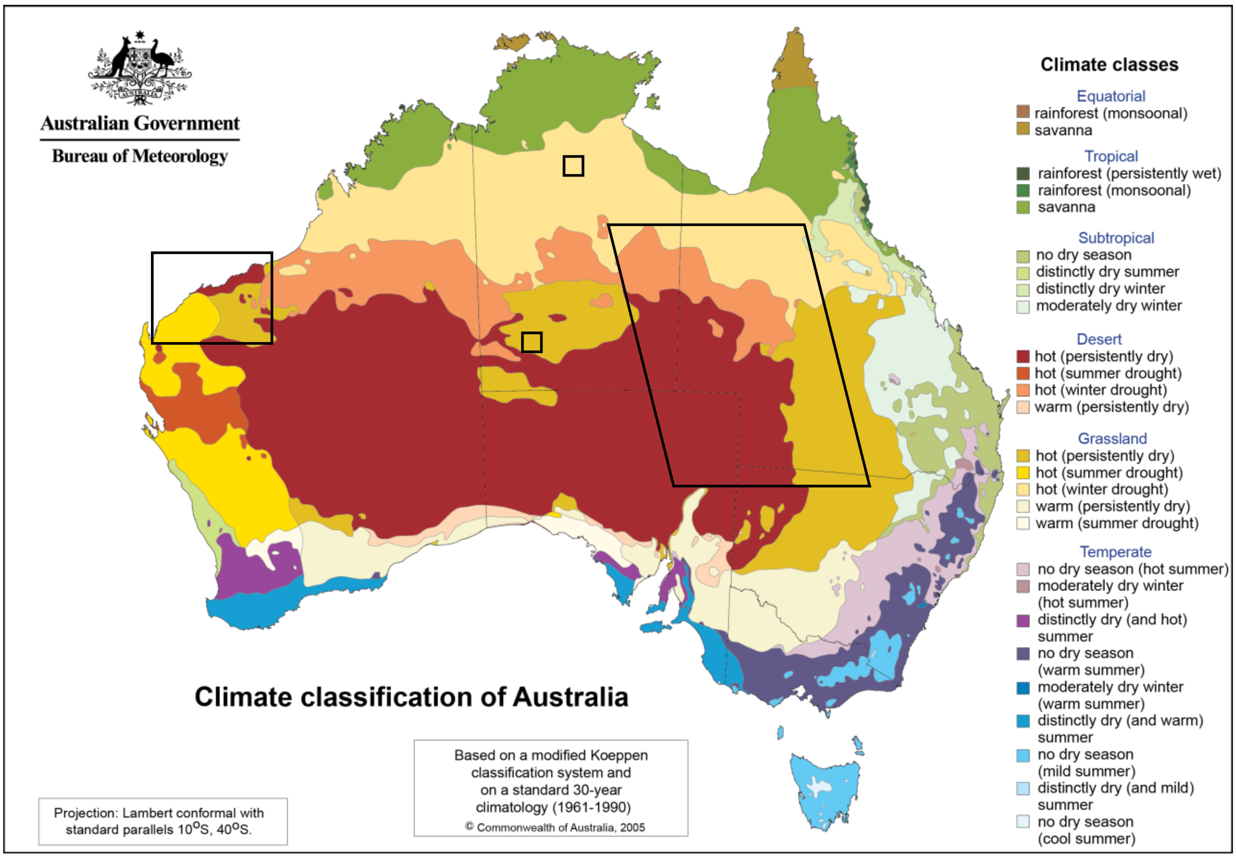

Figure 1.1 Areas of nest site locations recorded from 2003 to 2013 (n = 32) (enclosed in black quadrangles), involving 41 breeding events. Base-map showing climate classification classes of Australia by Stern et al. (2000) provided by and copyright of the Australian Bureau of Meteorology (http://www.bom.gov.au).

Table 1.1 Published Grey Falcon records from Papua New Guinea (PNG). Each alleged identification concerns a single individual; sex and age were not reported.

Observer / reference	Date of observation	Approximate location	Circumstances
Finch (1981)	01/11/1980	Aroa Plains, c. 80 km NW of Port Morseby	mainly from moving car, with the naked eye
Stronoch (1981)	08/11/1980	Bulla Plains / Bensbach River, extreme SW of PNG	from aircraft, conducting aerial survey for deer
Stronoch (1981)	25/11/1980	Bulla Plains, c. 8 km south of the previous location	100 m distance, with binoculars
Harrison (2000)	April 1992	Bensbach River	20 m distance, from boat

Movements

The species' movements are poorly known (for an overview see Marchant and Higgins (1993)). Published views encompass the spectrum of movement patterns from sedentary

(Hobbs 1961) to at least partly sedentary (Olsen and Olsen 1986, Chan 2001, Janse et al. 2015), regular seasonal movements (Olsen and Olsen 1986, Baker-Gabb and Fitzherbert 1989, Mooney 1998, Garnett and Crowley 2000), partially migratory (Chan 2001), partially nomadic (Morris et al. 1981), nomadic (Storr 1973, Hollands 1984), highly nomadic or irruptive (Reid and Fleming 1992), and movements triggered by environmental conditions (Bravery 1970, Olsen and Olsen 1986, Smith et al. 1995, Garnett and Crowley 2000), but without much direct evidence. Such variation in interpretation of movements for a species is, however, common for Australian arid zone birds (Pavey and Nano 2009).

Some individuals of the species undertake movements that may best be described as nomadic, as the following examples suggest.

(i) Morse (1922) recorded the avifauna in the District of Moree in northern NSW over a period of 13 years, and encountered Grey Falcons on only one occasion (year and date not provided); the record was for a group of five closely associated individuals, presumably a family group (see below).

(ii) Aumann (2001a) surveyed the breeding of raptors in an area of about 45 000 km^2 near Papunya west of Alice Springs in the Northern Territory (NT). Between 1994 and 2014 he reported breeding by Grey Falcons in two years only; two breeding pairs in 1997 (Aumann 2001b) and one in 2011 (T. Aumann pers. comm. 11 June 2015). Subsequent searches by T. Aumann in 2012 and myself in 2013 failed to locate Grey Falcons in that general area.

(iii) Martin and Royal (2001) reviewed records of the Grey Falcon in central western NSW 1980–1999. The species was recorded there only once or twice per year for 1980–1983, but not for 1984–1992. For 1993, records included the only breeding event reported for that area over the entire period of 1980–1999 (Debus and Rose 2000). For 1999, Grey Falcons were recorded on three occasions involving five birds in total, contributing to a total of eight birds from NSW for that year, the highest number in a year for NSW at that time. That area was affected by a short but severe drought in 1982, followed by average conditions 1983–1993, a drought in 1994, and well above average rainfall in 1998 and 1999 (Liddy et al. 2014). This suggests that the species was very scarce or absent during unfavourable conditions and that individuals reappeared when conditions had started to improve.

(iv) For the Strzelecki Creek region in north-eastern South Australia, an area visited regularly by bird watchers and especially during parts of the breeding season, Falkenberg (2011) reported breeding four times during the 10 seasons he surveyed the area, 1982–85 and 1995–2000, with one breeding event each for 1982, 1984, 1996 and 1998. For the seven seasons 2003 to 2009, no published or unpublished breeding records are available. This latter period coincided with persistent drought in that area, ending in November 2009 (Liddy et al. 2014). In the breeding season following the end of that drought, 2010, a pair bred successfully in the Strzelecki Creek area (Schoenjahn, pers. obs.), again suggesting that the species abandons areas during unfavourable conditions and returns when conditions have improved.

Most other statements concerning movement patterns of Grey Falcon have been based on incidental sightings, short-term observations or unsubstantiated secondhand reports. The following three examples illustrate this point.

(i) Claims of the species being partly sedentary (Olsen and Olsen 1986, Chan 2001) were based on Hobbs (1961, p. 37) stating that 'there is a resident pair on Bundyulumblah station', a pastoral property in the Riverina district, central southern NSW. However, Hobbs (1961) provided no information as to whether the pair bred at all or in which of the breeding seasons between 1954 and 1959 (inclusive) breeding was recorded. The same critique applies to a claim by Witte (cited by Janse et al. 2015) who maintained that Sturt National Park in NSW holds three resident pairs of Grey Falcon.

(ii) The claim that individual Grey Falcons undertake seasonal movements north during autumn and winter (Olsen and Olsen 1986) has been pointed out to be potentially biased by the movements of bird watchers contributing to atlas surveys (Blakers et al. 1984, Baker-Gabb and Steele 1998, Martin and Royal 2001). Further, that reports of these autumn northward movements should pertain predominantly to young birds (Olsen and Olsen 1986) is incomprehensible, because at that time the subtle fieldmarks that allow to identify a one year old Grey Falcon in the field were not known at that time (Schoenjahn 2010b).

(iii) Claims that the species uses drought refuges (e.g., Marchant and Higgins 1993) were based on a report from the junction of the Murray and Darling rivers from winter 1967 (J. Hobbs, *in litt*. to Olsen and Olsen 1986), which seems to have involved one or more family groups (see below). Unfortunately no further details were provided. Similar concentrations of Grey Falcons during the severe inland drought from 2002/2003 to about November 2009, for example, have not been reported in the literature.

In summary, the reliable evidence indicates that Grey Falcons undertake nomadic movements but may remain absent from formerly occupied areas for extended periods even after conditions have become favourable again.

Food

Grey Falcons feed almost exclusively on birds while breeding, and also at other times (Cupper and Cupper 1980, 1981, Harrison 2000, Schoenjahn 2013). Prey species include doves, pigeons, small parrots and cockatoos, and finches, but a variety of other birds has also been recorded (Marchant and Higgins 1993, Schoenjahn 2013, Cook 2014, Fisher 2015). Non-avian prey recorded by direct observation include small mammals on three occasions (Schoenjahn 2013, Moore 2016) and a lizard (Czechura 1981). In stomach contents of Grey Falcons, Gray (see Condon and Amadon 1954, p. 234) found 'flesh and hair of a mouse-like creature', and Hall (1974) found mammal fur (and a quartz stone); further details were not provided. Invertebrate and other non-avian animal matter (e.g., earthworm) found in stomach contents and pellets (e.g., Barker and Vestjens 1989; Johnstone and Storr 1998) may have originated from stomach or crop contents of prey animals.

Body masses of positively identified food items recorded by direct observation ranged from 12 g (Zebra Finch *Taeniopygia guttata* (Smith 1983, Schoenjahn, pers. obs.); see Higgins (1999) for body mass) to about 300 g (Galah *Eolophus roseicapillus* (Cupper and Cupper 1981); see Higgins et al. (2006) for body mass).

Many food items that have been listed for the Grey Falcon (e.g., in summaries of Czechura and Debus (1985), Olsen and Olsen (1986), and Marchant and Higgins (1993)) lack confirmation or are otherwise questionable. Those lists included many bird species on the basis of inconclusive reports, for example concerning mock attacks, or on reports with questionable identification of the raptor (e.g., the Feral Chicken *Gallus gallus* reported by North (1912) may have been taken as prey by a misidentified accipiter), while most other animals remain unconfirmed, for example insects, especially grasshoppers (Hobbs 1961, McGilp 1934, Wright 2005), snakes (North 1912), rabbit kittens (Olsen and Olsen 1986), and rabbits (McGilp 1934). Also questionable are claims of carrion as food of Grey Falcons (e.g., Olsen and Olsen 1986, Marchant and Higgins 1993, Garnett and Crowley 2000). These claims are likely to stem from the known behaviour of Grey Falcons to often feed on their prey on the ground (Cameron 1932, Czechura 1981, McAllan 2013, Cook 2014), including verges of outback roads and tracks (Fisher 2015, Schoenjahn pers. obs.). A further source of those claims may be misidentification of the raptor. For example, pale individuals of Brown Falcon *F. berigora* are readily confused with Grey Falcons (Schoenjahn 2010b). These pale Brown Falcons are most common in Australia's arid interior and some authors considered these a distinct subspecies, namely *F. b. centralia* (Mathews 1916, Howard and Moore 1991). Of note, Brown Falcons are known to often take orthopterans, and feed occasionally on carrion (Storr 1980, Baker-Gabb 1984).

Breeding

No major studies had been conducted on the breeding behaviour of the Grey Falcon (Marchant and Higgins 1993), notwithstanding that observations of nesting Grey Falcons were published more recently (e.g., Falkenberg 2011). We do know, however, that these birds do not build their own nests (Marchant and Higgins 1993, Schoenjahn 2013), in line with all other members of the genus *Falco* (Brown and Amadon 1989). Nevertheless, earlier reports suggested that they do so (North 1912, Beruldsen 1980). They use old nests of other birds, mainly corvids and other raptors (Schoenjahn 2013), but probably not those of the Wedge-tailed Eagle *Aquila audax* (Brown and Amadon 1989, Olsen and Olsen 1986), because this claim has not been confirmed. During 2003–2014, I established that the species is univoltine and uses stick-nests of other birds in trees but also those on artificial structures such as telecommunication towers and power-line pylons (Schoenjahn 2013).

Breeding takes place from June to November, i.e. between mid to late winter and the end of spring, and therefore is in line with most congeners and indeed most raptors. Clutch size was reported in Olsen and Olsen's (1986) summary as 2–4, and nestling numbers were reported as 1–4 (Schoenjahn 2013). The incubation period is 35 days (Cupper and Cupper 1980, Hollands 1984) and the nestling period 49–52 days (Cupper and Cupper 1980). There is no evidence for siblicide, in line with other members of the genus (Cade 1982).

Social organization

The species is considered monogamous and the sex ratio of the population is not known (Marchant and Higgins 1993). The only hint of any social organisation involves members of a family of Grey Falcons said to be staying closely together as a group 'perhaps until the next breeding effort of the adults' (Olsen 1995, p. 167, Marchant and Higgins 1993, Debus

1998). However, no details or evidence were provided. At that time, i.e. in the 1990s, only one relevant record had been published, a secondhand report mentioned in the photographic book “Hawks in Focus” (Cupper and Cupper 1981) (Table 1.2). The oldest such record (No. 1 in Table 1.2) involved an adult and a juvenile bird that were shot while soaring together by a member of Captain Sturt’s expedition party (see Schoenjahn (2010a) for further details), the remaining records (Numbers 2–4 in Table 1.2) are firsthand, undisputed records.

Table 1.2 Published records of groups of Grey Falcons presumed to be family groups, each comprising one or more adults (ad.) in company of one or more juvenile birds (juv.). The 12th of October was the median fledging date established in the present study (see text).

	Month of the year	No. of months after 12 Oct.	Number and age of birds	Reference
1	May	7	1 ad., 1 juv.	Sturt (1849, see Schoenjahn (2010a))
2	May	7	2 ad., 2 juv.	Dennett and Abbotts (2008)
3	May	7	2 ad., 1 juv.	Schoenjahn (2011b)
4	June	8	2 ad., 1 juv.	Martin and Royal (2001)
5	Oct.	12	2 ad., 2 juv.	Cupper and Cupper (1981)

As is typical of reports on Grey Falcons, contradictory statements in regard to the social behaviour described above have been made. McGilp (1934, p. 277) wrote that the species ‘does not attend to the wants of its young or allow them to remain in the vicinity of the nest for very long.’ This statement appears arbitrary, as do other claims by that author (Debus 2015).

Threats

Garnett et al. (2011, p. 150) summarized the threats to the species, as suggested by previous authors, noting that ‘all threats to the Grey Falcon are speculative.’ Indeed, none of the threats that have been proposed to date were substantiated by their original author(s), probably because the propositions were not based on focused studies of the species but stemmed from general considerations, such as human-induced habitat alterations (Garnett and Crowley 2000, Garnett et al. 2011). This situation of speculating about threats is typical for threatened species in Australia (C. Pavey pers. comm. 1 Apr. 2016). Egg-collection was undoubtedly a threat until about the late 1980s (Cupper and

Cupper 1981, Hollands 1984, Dennis 1986, SAOA 1992), but may not be of such importance any more.

The species' population size of an estimated <1000 mature individuals (see above) was the basis for classifying the species as "Vulnerable D1" (Garnett et al. 2011). This view was subsequently acknowledged by BirdLife International (2016, 2017). An important threat to the species as a whole (as opposed to its individuals directly) therefore lies in the extremely low population size *per se*. Indeed, small populations are expected to have an increased probability of extinction compared to large populations (Traill et al. 2010). Being spread thinly over a vast area, the Grey Falcons' movement abilities may therefore be of pivotal importance. That is, a high mobility would allow them to respond to environmental challenges, for example by abandoning areas that have become unsuitable for breeding or survival, and to evolutionary challenges, for example by enabling the individuals to interbreed randomly within the entire population to combat losses of genetic variation by gains through mutation. A loss in genetic variation, an effect of finite population size, may reduce a population's ability to respond to future environmental changes (Lande 1988, Frankham 1995). In consequence, an understanding of the movements of Grey Falcons is indispensible to identify threats to the species and propose meaningful conservation measures.

Phylogeny and origin of the Grey Falcon

The phylogenetic relationships within the speciose family Falconidae (caracaras, forest-falcons, falcons) and the estimated ages of its species have been the subject of debate for decades (e.g., Fox 1977, Cade 1982, Schodde 1982, Helbig et al. 1994, Griffiths 1999, Wink and Sauer-Gürth 2004, Hackett et al. 2008, Ericson 2012, Zhan et al. 2013). The most recent and most comprehensive contribution is that of Fuchs et al. (2015). Those authors analysed eight independent nuclear and mitochondrial loci from each of the 64 hitherto recognized Falconidae species, and proposed a new phylogeny for that family that recognizes 65 species, including 40 species in the genus *Falco*.

According to the latter phylogeny, the Grey Falcon *F. hypoleucos* is a member of a group comprising 11 species (Figure 1.2). Of these, the Red-necked Falcon *F. chicquera* diverged first. After that the divergence took place between the Prairie Falcon *F. mexicanus* and the other seven species. Of these latter, the Grey Falcon diverged first, and then the divergence of two species groups took place, those that make up the *Hierofalco* group *sensu* Wink and Sauer-Gürth (2004) (Lanner Falcon *F. biarmicus*, Laggar

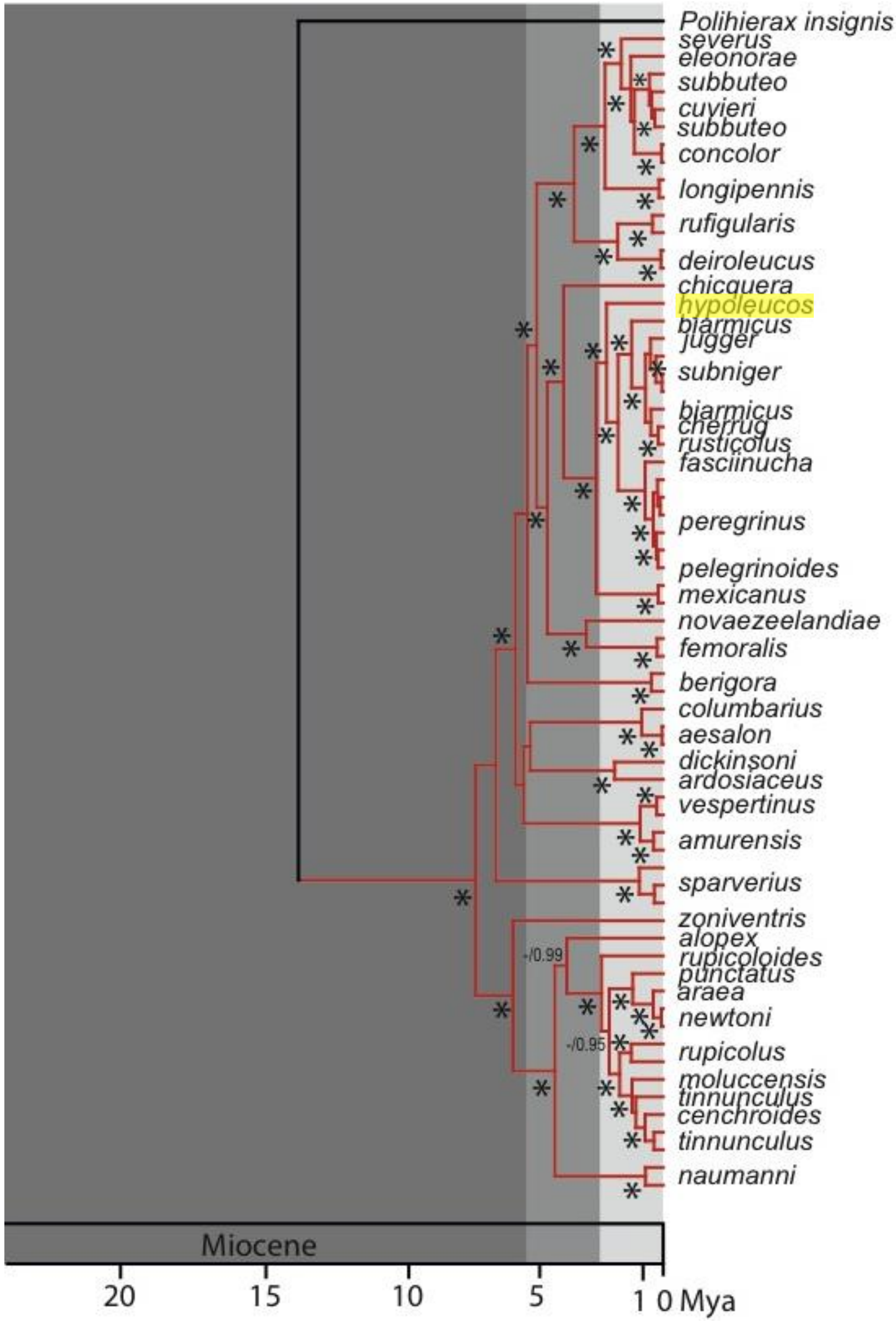

Figure 1.2 Chronogram of the *Falco* clade based on eight nuclear loci (adapted from Fuchs et al. 2015, p. 173), with *Polihierax insignis* as the designated outgroup. Asterisks indicate posterior probabilities and maximum likelihood bootstrap support values higher than 0.95 and 70%, respectively. Yellow highlight indicates Grey Falcon. Used with permission.

Falcon *F. jugger*, Saker Falcon *F. cherrug*, Gyrfalcon *F. rusticolus* and Black Falcon *F. subniger*) and those in the peregrine complex (Peregrine Falcon *F. peregrinus* and Barbary Falcon *F. pelegrinoides*) plus the Taita Falcon *F. fasciinucha*. The Grey Falcon thus shares a common ancestry with these latter two groups of species and is not phylogenetically close to any one species.

Fuchs et al. (2015) suggested further that the Grey Falcon diverged from its closest relative about 1.4–2.8 million years ago (mya). For Australia's Black Falcon the respective divergence was given as 0.1–0.50 mya, and for the Australian subspecies *macropus* of the Peregrine Falcon 0.08–0.3 mya (from Fuchs et al. 2015, p. 178).

To construct their best estimate phylogeny, however, Fuchs et al. (2015) used only eight loci, and the analyses of each of three subsets of the eight loci and also of the individual genes gave different results with only moderate bootstrap support in most instances. In consequence, disentangling the phylogenetic relationships within *Falco* may require more than eight loci, the difficulty of the task reflecting the relatively recent (within the last 8 million years) and rapid diversification of this genus (Fuchs et al. 2015).

In regard to the geographic origin of the Grey Falcon, Schodde (1982, pp. 202–204) hypothesized that Australia's two desert falcons, Black Falcon and Grey Falcon, are part of an 'autochthonous Eyrean' avifauna, or, 'if they did originate beyond Australia, they almost certainly arrived a long time ago', without indicating a time. Fuchs et al.'s (2015) best estimate phylogeny and chronogram does not answer the question as to whether the Grey Falcon arrived in Australia as a full species. However, the ancestor common to *F. hypoleucos* and its sister clade may have diverged from the ancestor of *F. mexicanus* as recently as 3 mya (Fuchs et al. 2015). At that geological time the Australian continent was nearing its present global position, its climate was generally becoming drier (notwithstanding continuous rapid changes in the climate between cooler interpluvial phases and warmer pluvial phases), grasslands were spreading, and Budgerigars, an important food for Grey Falcons (Schoenjahn 2013), had already appeared (Australian Museum 2002). Thus, either the Grey Falcon evolved in Australia in response to these changes, or the species evolved elsewhere, in the arid zones of central or western Asia perhaps, and arrived subsequently in Australia. Upon arrival in Australia the Grey Falcon or its ancestor would have encountered climatic conditions and habitat very similar to the species' environment at present.

Summary

The ecology of the Grey Falcon is known almost entirely from anecdotal and opportunistic observations and from my preliminary investigations that led to this study. Despite this limitation, the species is clearly one of the rarest species of *Falco* in the world, and it is unique among its Australian congeners in (i) persisting exclusively in the arid and semi-arid zone, an environment that is characterised by unpredictable and extreme periods of boom and bust and in having the highest average annual temperatures in Australia, and (ii) in having the most restricted diet of that group, comprising almost exclusively of birds. Further, the species' spatio-temporal distribution suggests that individuals may be nomadic to some degree, a behaviour that is unusual among members in the genus *Falco* (Appendix 2).

Despite our limited understanding of the Grey Falcon's ecology and origin it is clear from the reliable information that is already at hand that a key element in explaining the species' ecology is the extreme and unpredictable climate of the environment that the species inhabits.

1.4 Living in an environment typified by pulsed resources

The occurrence of the Grey Falcon is largely confined to Australia's arid and semi-arid zone (Chapter 1.3). Arid and semi-arid environments are governed predominantly by precipitation events that are unpredictable in occurrence, duration and productiveness (Noy-Meir 1973). However, the level of unpredictability in rainfall varies across the world's arid zones. On a global scale inter-annual rainfall is most variable in northern and central Australia (north of latitude 27º South) and other low-latitude arid regions (van Etten 2009), and so is most unpredictable in these regions. Longer-term studies comparing, for example, inter-decadal rainfall variability of the world's arid zones are unavailable. It is known, however, that Australia's arid zone experiences droughts that may last up to five and more years. An example of this is the Federation Drought of 1895–1902 which affected most of Australia (Bureau of Meteorology 2017). This situation and the consequences for animals that persist in Australia's arid zone are exemplified by a study of small mammals in the western Simpson Desert, central Australia, estimating that mammal population densities remain low for 8.5 years per decade (Pavey et al. 2014).

Arid environments with unpredictable precipitation are driven by the pulsed availability of moisture from these events. These pulses of moisture in turn produce pulses in primary productivity as plants respond by germination and growth. Invertebrate and vertebrate animals are adapted to these pulses of resource availability in a variety of ways (for an overview see Pavey et al. 2015). Organismal adaptations that have evolved in response to these resource fluctuations include dormancy (e.g., many invertebrates, Crawford 1981), aestivation (e.g., burrowing frogs, Hillman et al. 2009), irruptive movements into areas of the arid zone following heavy precipitation events (Dean 2004), possibly with subsequent reproduction (e.g., Banded Stilt *Cladorhynchus leucocephalus*, Pedler et al. 2014), and the use of refuge areas located within the respective species' usual arid zone distribution area (e.g., Plains Mouse *Pseudomys australis*, Pavey et al. 2014).

The Grey Falcon has a breeding distribution restricted to areas within the hottest climate classes (Schoenjahn 2013, and Figure 1.1), i.e. areas of extreme and unpredictable arid environments that are typified by pulsed resources as described above. This circumstance can be expected to be reflected in adaptations related to the species' breeding ecology, movements (which may be nomadic), and also to behavioural, morphological, anatomical, and physiological characteristics. Further it may be expected that the extreme climate imposes considerable threats to the Grey Falcon. Climate has already been suggested to be a key factor in explaining the species' scarcity (Schoenjahn 2013).

1.5 The research questions addressed in the thesis

How do individuals, during the various stages of their lives, cope with extremely high ambient temperatures? I explore this question in Chapter 2, by investigating whether the species is specifically adapted behaviourally and anatomically to its environment. I do so by comparing, across selected *Falco* species, behavioural and anatomical characteristics that have the potential to aid the individuals of Grey Falcon to cope with their extreme environment. In particular, I studied their activity levels in key situations including nest defence, feeding of nestlings, and flight modes, and also characteristics of their plumage that have the potential for aiding the individuals to cope with the heat.

The breeding ecology of a species is of particular interest because activities related to breeding dominate the lives of reproductively active birds for considerable time in most years and are energetically costly. These activities include mate seeking, courtship, nest selection, laying, incubation, and, in altricial and semi-altricial species such as falcons, caring for nestlings and fledglings (Cade 1982). In the Grey Falcon, this period lasts several months, the period from egg laying to fledging alone being about three months (see above). In general, univoltine bird species (such as falcons) are expected to have breeding periods that coincide with the period most favourable to raise their young (Lack 1966). For raptors this is typically the period of most abundant food (Newton 1979). Seemingly in contrast, Grey Falcon young fledge at the onset of summer, a time when unpredictable and extreme climatic events may hamper continuous food acquisition (see above) and thus may reduce the survival chances of the fledglings. However, my observations of Grey Falcons indicated, quite early in my investigation, that the breeding ecology of these birds includes a behaviour unique among birds of prey, that of extended juvenile dependence (see section on social organization above). In Chapter 3 I therefore investigate whether the species' breeding ecology, and particularly the extended juvenile dependence, could be explained as an adaptation to the extreme and unpredictable climate that typifies the species' environment. I also investigate how parents support their young during that period and the extent to which they do this. I test whether juvenile dependence in Grey Falcons is as extended as the available literature appears to indicate.

The movement of individuals is a further key aspect in the ecology of a species, particularly so in species living in desert environments (Dean 2004). The Grey Falcon lives exclusively in an area where at least 45% of the regularly breeding bird species are considered to be nomadic, the highest proportion among the arid and semi-arid regions of the world by a considerable margin (Dean 2004, in particular Table 2.3, p. 21). This leads to the question, are Grey Falcon nomadic? Further, the species' diet throughout the year consists predominantly of nomadic bird species, for example Diamond Dove *Geopelia cuneata*, Peaceful Dove *Geopelia striata*, Cockatiel *Nymphicus hollandicus*, Budgerigar *Melospittacus undulatus*, and Zebra Finch (Schoenjahn 2013, and Chapter 1.3). Therefore I test, in Chapter 4, whether the Grey Falcon is nomadic and whether short- and long-term movements of this highly mobile species can be explained as adaptations to its environment.

In Chapter 5, I discuss putative threats that were proposed by previous authors and those that emerged during the course of fieldwork during this PhD research. Conservation measures to ameliorate threats and to improve the conservation status of the Grey Falcon are proposed. A threat to the species as a whole stems from its small population that is spread across a massive area (Schoenjahn 2013). This may make the Grey Falcon vulnerable to demographic stochasticity (*sensu* Frankham and Ralls 1998, Traill et al. 2010). I test whether its extremely large distribution and mobility help the species as a whole to persist by evading adverse conditions that affect parts of its distribution but, presumably, never all of it. Further, the Grey Falcon may be impacted by climate change which has not been proposed previously. The species' apparent specialisation to an arid hot environment may render individuals, and the species as a whole, vulnerable to the unpredictable and extreme climatic events that characterize this environment. Climate predications for Australia's (hot) arid zones include increases in frequency and intensity of extreme climatic events, heat waves and deluges of rain for instance, and in year-round temperatures (Watterson 2015). These changes may challenge the Grey Falcon physiologically and behaviourally and may also have a major impact on its prey base.

Chapter 6 is a synthesis that brings together the challenges that the environment exerts on the individuals of the Grey Falcon and the ways in which the species is adapted to these challenges. Having investigated in this thesis key aspects of the ecology of these organisms, namely food acquisition, reproduction, and movements, I examine whether the interpretations of the respective findings have a specific element in common. If so, this would suggest that the ecology of the Grey Falcon in general is governed by that common element.

This thesis is written as a series of stand-alone journal manuscripts, and as such there is some repetition of material between different Chapters.

Chapter 2

Some like it hot – adaptations of an Australian arid-zone endotherm, the Grey Falcon *Falco hypoleucos*

2.1 Introduction

Hot deserts are among the most challenging environments inhabited by terrestrial organisms because they have to contend with high air temperatures, intense solar radiation, and surface water being scarce and unpredictable (Fisher et al. 1972). Nevertheless, even the hottest deserts are inhabited by endothermic animals, including mammals and birds (e.g., Keast 1959, Pavey and Nano 2006). For these, effective thermoregulation mechanisms and the maintenance of physiological water levels are critical in arid hot environments. The animals are affected by external and internal heat sources that include hot air that surrounds (and is inhaled by) them, direct solar and secondary radiation (e.g., from the ground), and the heat produced by their own metabolism. Processes that increase metabolism above its basal rate, and thus increase the production of metabolic heat, include physical exercise of the skeletal muscles, digestion of food, and thermoregulation during heat stress (Baldwin and Kendeigh 1932, Dawson 1954, Weathers 1981).

The ways in which birds cope with these challenges have attracted research interest over a long time from a diversity of scientific disciplines, including behavioural ecology, morphology, and physiology. Behaviours that help desert-living birds to lessen or evade the impact of desert heat include shade-seeking, burrowing, reducing activities when it is hottest, changing posture relative to the sun or wind, and moving to distant areas with more favourable conditions (Bartholomew and Dawson 1954, Adolph 1964, Walsberg 1982, Williams and Tieleman 2005). Morphological adaptations of desert living in birds include, for example, the feather structure in sandgrouse (Pteroclidae) that facilitates the transport of water in the adults' belly feathers to their chicks (de Juana 1997) and, in desert-living owl species (Strigiformes), the sparse feathering of the toes that facilitates the loss of body heat to the environment in comparison to most owl species found in colder climate zones (Kelso and Kelso 1936).

Physiologically, the most intuitive way by which endothermic animals combat high body temperatures is by evaporation of water from the respiratory system and across the skin. In consequence, aridity is a major challenge for most desert-living organisms and particularly for endothermic animals, including birds (e.g., McKechnie et al. 2016). Insectivorous and carnivorous birds, however, are largely independent of surface water, and this appears to be true also for species in the genus *Falco* (Bartholomew and Cade 1957). Although these birds may drink water when it is available, they are able to survive solely on the water acquired through their diet (Fisher et al. 1972). Therefore, the availability and accessibility of suitable food resources is crucial to these organisms.

Because birds lack sweat glands their evaporative cooling mechanisms are limited to respiratory evaporation and insensible cutaneous perspiration. The latter is a process of passive diffusion through the epidermis (Marder 1983). However, the body of birds is generally well insulated with feathers, which hampers the passage of water vapour (Schmidt-Nielsen 1964). Therefore, cutaneous cooling is generated predominantly at the areas of exposed skin, the unfeathered parts of the tarsometatarsi being of primary importance (Schmidt-Nielsen 1964), and this appears to be true also for members of the genus *Falco* (Mosher and White 1978).

The sparsely feathered and thus poorly insulated sides of the body and the underside of the wings are also areas of heat transfer from the body to the environment through radiation, conduction and convection (Bartholomew and Dawson 1954, Eliassen 1963). These areas are exposed when the wings are held away from the body, particularly during flight, but also at rest. The latter behaviour is commonly observed in desert-living birds when it is particularly hot and, especially, after activity (Bartholomew and Dawson 1954, Schmidt-Nielsen 1964).

Of particular help to desert-living birds are two characteristics that are found in most avian species, regardless of whether they live in the coldest or hottest climate zones of the world: a high regular body temperature, averaging between 40ºC and 41ºC, the highest regular body temperature among endotherms (Baldwin and Kendeigh 1932, Williams and Tieleman 2005), and the ability to tolerate, without injury, body temperature levels elevated by up to 4ºC (Dawson and Schmidt-Nielsen 1964). At rising air temperatures and increasing solar radiation these two characteristics delay the onset and reduce the degree of thermoregulation (Bartholomew and Dawson 1954).

Focused studies on adaptations to extreme climates, and especially to hot desert climates, in *Falco* species seem very scarce. They include Mosher and White's (1978) laboratory-based study on thermoregulation in four large species of *Falco* (Peregrine Falcon, Prairie Falcon, Laggar Falcon, and Lanner Falcon). Those authors found that, in these birds, the unfeathered parts of the tarsometatarsus play a possibly important role in thermoregulation, in line with other species of birds (e.g., Schmidt-Nielsen 1964). Specifically, Mosher and White (1978, p. 84) found that, in the species they studied, 'the extent of bare tarsus shows good correlation with thermal habitat'. Similarly, for the arctic Gyrfalcon, Cade (1982, p. 74) noted that its tarsi are 'densely feathered on more than the upper half, often with a scattering of inconspicuous feathers lower down, a detail found in no other species of *Falco* and obviously associated with life in cold climates.' Further, Cade (1982, p. 74) stated that in Gyrfalcons, 'down and other fluffy, insulative structures are highly developed.' Potapov and Sale's (2005, p. 64) claim, however, that Gyrfalcons shed or pluck moulting down feathers in hot weather to aid thermoregulation seems to lack supportive published observation data. For the Peregrine Falcons inhabiting the wet Pacific coast of British Columbia and south-eastern Alaska, Brown and Amadon (1989, p. 37 ff) asserted, without providing a reference, that these birds are exceptionally protected against rain by a filmy bloom on the feathers that makes these birds 'as waterproof as a duck'. Evidently, autecological studies into the adaptations of falcons to extreme climates are warranted.

The study species, Grey Falcon *Falco hypoleucos*, is a rare and little known Australian endemic raptor. It is distributed sparsely over Australia's arid and semi-arid zone (Schoenjahn 2013), an area of about 5 million km^2 (Australian Museum 2002; Pavey and Nano 2006), covering about 70% of the Australian mainland. It is a medium sized falcon. The median body mass of adults captured from the wild was 412 g (n = 7; range 339–448 g) for males, and 502 g (n = 9; range 486–582 g) for females (Schoenjahn, unpublished data). Grey Falcons of all ages feed almost exclusively on birds throughout the year (Schoenjahn 2013). They breed no more than once a year, invariably between July and November (Chapter 3).

In this chapter I test the hypothesis that the Grey Falcon is specifically adapted to its life exclusively in areas of the hot arid and semi-arid zones of the interior of the Australian continent. I do so by examining the activity levels of the Grey Falcon and then comparing these with equivalent details from the well-studied Peregrine Falcon *F. peregrinus*. Preliminary behavioural observations in the field suggested that Grey

Falcons often, for example, seek thermal updrafts when leaving the nest rather than using active wing-beating flight, and that they do not pursuit prey but stoop at the target typically only once and then give up regardless of the outcome. In addition, I compare, across a selected group of *Falco* species, specific plumage characteristics that I predict aid Grey Falcons cope with high heat loads.

2.2 Methods

Behaviours

Behavioural data from wild Grey Falcons were collected between July 2003 and November 2016. The general methods and study area have been described by Schoenjahn (2013). I recorded for Grey Falcons of all ages, i.e. nestling to adult, behaviours that I considered to be key to tolerance of high heat loads. Behaviours included flight mode, hunting method, perseverance and success, defence of the active nest and territory, and the temporal distribution over the course of the day of feeding events involving adults or nestlings at or near nests containing eggs or young, and potential thermoregulatory behaviours.

Flight mode of adults leaving the nest or roost site was recorded together with the time of day, direction of the flight path relative to the direction of the wind, and wind force. Three flight mode categories were distinguished: soaring with very few or no wing-beats, wing-beating whilst updrafts were unavailable, and wing-beating against wind ≥3 Beaufort. Flight modes were assessed only in situations in which the behaviour of the bird(s) was unaffected by the observer. If both partners of a pair left the nest or roost site at the same time, both birds invariably used the same flight mode, and this was counted as a single incidence. Hunting method and perseverance of adult Grey Falcons were recorded to gain an understanding of the level of activity involved in this pivotal behaviour.

Hunting method was recorded as stoop, pounce, or tail-chase. Hunting success was calculated as the number of times a prey was caught divided by the number of pursuits involving one or more attacks.

Incidences of active nest defence, and the absence of such behaviour, by breeding Grey Falcons against intruders (birds in all cases) were also recorded. A lack of response to intruders (definition see below) was recorded only when the latter were within about 500 m of the nest, because those further away were never attacked. An ‘intruder’ was any bird of prey (Falconiformes) or corvid (Corvidae) because these were involved in all but one active agonistic interaction (the latter of which involved two Little Corellas *Cacatua* *sanguinea*). I used the same methods and definitions to record behaviours of non-breeding adult Grey Falcons (single or paired) toward intruders at regular roost sites. Any incidence of aggression (and the absence thereof) that involved both partners of a pair was counted as a single bout of behaviour and the activity level of the more active partner was recorded.

The feeding times at nests, a proxy for the hunting activities of the adults, were recorded to investigate at what times of the day the adults were most active. All observations concern nests with eggs or nestlings. I recorded all feeding events, i.e. parent-offspring and parent-parent feeding, and also individual adult partners feeding on their prey at the nest site. Only data from those days when virtually uninterrupted observations could be made from sunrise to sunset (outside this period feeding was never observed) were included in the analysis. In addition, I used only those periods when the falcons involved were considered undisturbed by my presence and activities. Some feeding events were undoubtedly not noticed, partly because, even at the nest, Grey Falcons are often silent (Schoenjahn, pers. obs.), and also because adults may have fed outside the observer's view. In addition, most nests involved were high above the ground (up to 100 m) on tall telecommunication towers (Chapter 1; see also Figure 2.1) which could have influenced the feeding behaviour of the adults, for example in regard to where they fed on their prey.

Potential thermoregulatory behaviours recorded include tracking of shade when perched, changing body posture in relation to the sun and wind, airing (facing the wind with wings held away from the body, wings often also lowered), panting (which was assumed when the bird was perched with its bill open for longer than 5 seconds), and shading of nestlings by their parents.

Environmental variables recorded during observations were air temperature (measured in full shade at about 1 m above ground with a key-ring thermometer by Recta of Switzerland), wind force (estimated according to the Beaufort scale for land areas (Royal Meteorological Society, https://www.rmets.org/weather-and-climate/observing/beaufort-scale)), and wind direction (determined with a hand-held compass model 'Starter 1-2-3' by Silva of Sweden).

Total observation time was 1799.75 hours, involving the adults of 94 (breeding and non-breeding) pairs or family groups (1773.25 hr, median 13.38, range 0.5–85.5), and eight single adults (26.5 hr, median 1.75, range 0.25–8.0). Because most birds were not marked for individual identification it is likely that some of these individuals and pairs were assessed in more than one year and therefore counted more than once, but this was unavoidable and its impact was lessened by the long study period of 14 years, the sampling of individuals over the entire distribution of the species, and the large number of individuals observed. The number of active nests that I monitored during 2003–2016 is 47, involving 31 individual sites across Australia.

Figure 2.1 Example of the landscape that surrounds a typical nest on a repeater tower.

The time format throughout this chapter is local solar time (LST). That is, for any given location 1200 hr LST was set to coincide with the zenith of the sun at the nearest quarter of degree longitude. The resulting precision is ± 30 seconds of time. This method allows the temporal comparison of observations made at locations across Australia irrespective of the longitude, time zone, and daylight saving time.

Note that data collection was not consistent and not systematic due to logistic constraints (Schoenjahn 2013). For example, access tracks became impassable during and after rain and often so for prolonged periods, and study sites had to be evacuated at the approach of inclement weather.

All field observations and measurements (see next section) were carried out solely by me. This ensured consistency in all aspects of data-recording.

Anatomical data from study skins

Morphological data from 10 specimens of Grey Falcon and a total of 105 specimens of 10 other *Falco* species from a range of climatic zones were taken at the ornithological collections of the Academy of Natural Sciences Philadelphia (ANSP), the American Museum of Natural History (AMNH), New York, and the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley (for details and accession numbers of all specimens concerned see Appendix 3). An overview and the grounds on which the 10 species were selected is provided in Table 2.1. Subsequently excluded from the analysis were the specimens of *F. peregrinus* labelled as pertaining to the subspecies *brookei* and *calidus* (see Appendix 3). The locations of their collection sites are outside of the respective subspecies' distribution area given by White et al. (2013), which renders the subspecies allocation questionable. Precision of the measurements and supplementary details are provided in Table 2.2.

Four parameters were measured respectively assessed visually: (i) the length of the longest feather on the side of the breast, i.e. of the medial pectoral tract or *pteryla pectoralis medialis*, (ii) the length of the unfeathered part of the tarsometatarsus, (iii) the length of the trousers or crural flag (*vexillum crurale*, see below) (terminology follows Lucas and Stettenheim (1972)), and (iv) the trousers' density.

The longest side feather was measured because in perched Grey Falcons facing the wind, long contour feathers on the sides of the breast are moved conspicuously by the wind. Because this may aid heat transfer from the body of these birds to the environment I compared the length of the longest side feather across species. The unfeathered portion of the tarsometatarsus was included in the investigation because in some species this area serves thermoregulation, including at high temperatures, as demonstrated for example in the Wood Stork *Mycteria americana* and in some New World vultures (Kahl 1963, Steen and Steen 1965, Hatch 1970). In cases where the extent of the feathering was unequal around the circumference of the tarsometatarsus, the average length was noted. Also measured were the lengths of the trousers, i.e. the parts of the plumage that are formed by feathers that emerge from the skin at the proximal end of the crus. In many raptor species these pennaceous contour feathers protrude beyond the intertarsal joint, in some even beyond the metatarsophalangeal joints. Because they may thus conceal part or all of the

Table 2.1 *Falco* species selected for comparison with the Grey Falcon *F. hypoleucos* and the criteria for the selection of each species for comparison with Grey Falcon. Diet, behaviour, and body mass follow White et al. (1994) unless indicated otherwise. Climate types pertain to the locations where the specimens were collected, or, for the two strictly migratory species, *F. eleonorae* and *F. concolor*, to the respective species' typical wintering / summering areas according to White et al. (1994). See Appendix 3 for details of the specimens. Fields were left blank if the feature was not taken into consideration when selecting the species (e.g., *F. jugger* was select for the climate type, regardless of its diet).

Falco species	n	Diet	Behavioural aspects	Climate types *	Body mass (g) **
hypoleucos	10	Virtually exclusively birds [1]	Not migratory; low-energy hunting [2]	Arid–hot	♂: 412 [3] ♀: 502 [3]
chicquera (incl. *ruficollis*)	6			Arid–hot, Tropical	♂: 170 ♀: 248
eleonorae	4	Dissimilar (flying insects; when breeding, birds)	Dissimilar (migratory, hunting methods)	Temperate–warm or hot summer, Arid–hot, Tropical	♂: 350 ♀: 388
concolor	4	Dissimilar (flying insects; when breeding, birds)	Dissimilar (migratory, hunting methods)	Arid–hot, Temperate–warm or hot summer, Tropical	♂: 267 [4] ♀: 289 [4]
deiroleucus	4	Somewhat similar (flying prey)	Dissimilar (hunting methods)	Temperate–warm summer, Tropical	♂: 339 ♀: 605
subniger	4		Similar (hunting methods) [2]	Arid–hot, Tropical	♂: 610 ♀: 805
biarmicus	4			Temperate–hot summer, Arid–hot	♂: 550 ♀: 800
jugger	5			Arid–hot	♂: 606 ♀: 769
rusticolus	12			Polar	♂: 1141 ♀: 1681
mexicanus	6			Cold–warm summer, Arid–cold	♂: 575 ♀: 838
peregrinus	56	Similar (mainly birds)	Dissimilar (hunting methods) [5]	All temperature classes	(not used)

* Köppen-Geiger climate classification after Peel et al. (2007).
** If the source provided a range for each sex, then the arithmetic middle value (rounded to the nearest gram) of each range was used. In cases where a range was given for the sexes combined, then the lower half of that combined range was taken as the range for the male body mass, and the upper half as the range for the female body mass; from these hypothetical ranges the arithmetic middle values were used.
[1] Schoenjahn (2013).
[2] This study; see Table 2.3.
[3] Schoenjahn, unpublished data; see text.
[4] M. McGrady (International Avian Research, Austria), pers. comm. 21 Feb. 2017.
[5] See text.

Table 2.2 Methods of measurements taken from museum specimens (study skins) held in the wildlife collections of AMNH, ANSP, and MVZ (see text, and Table 2.1). 'Tarsus', tarsometatarsus. Measurements No. 1–6 were taken to determine the sex of the specimen (see text).

	Measured item	Instrument	Precision	Comment
1	Wing length	Ruler, flexible, metal, butted	Nearest mm	Straightened and flattened as much as possible
2	Tail length	Ruler, metal	Nearest mm	See Baldwin et al. (1931)
3	Exposed culmen	Vernier calliper	Nearest 0.1 mm	Chord of exposed culmen without cere
4	Culmen + cere	Vernier calliper	Nearest 0.1 mm	Chord of exposed culmen with cere
5	Middle claw	Vernier calliper	Nearest 0.1 mm	Chord of the claw of digit III
6	Hind claw	Vernier calliper	Nearest 0.1 mm	Chord of the claw of the hallux
7	Length of longest side feather	Ruler, metal	Nearest mm	See text
8	Tarsus length	Vernier calliper	Nearest 0.1 mm	See Baldwin et al. (1931)
9	Length of unfeath. part of tarsus [1]	Vernier calliper	Nearest 0.1 mm	See text
10	Length and quality of trousers [2]	Visual	Estimate [2]	See text

[1] See text for further details concerning this measurement, especially in regard to the circumstance that the lateral side of the tarsometatarsus may be feathered further down, i.e. further toward the toes, than the rest of the tarsometatarsus.
[2] See text for definition of "trousers" and the method of their assessment.

tarsometatarsus, especially when the bird is perched in still air, these parts of the plumage are colloquially called trousers. The trousers may have thermoregulatory effects in providing shade and wind-protection to the lower leg and even the toes. The length of the trousers was established by visual comparison with the length of the tarsometatarsus, and was recorded as a fraction (e.g., ¼, ½, ⅔) of the length of the tarsometatarsus. The trousers' density was assessed qualitatively in regard to their potential thermoregulatory effect and recorded in terms of being thin, thick, or bushy. Differences in the length and structure of the trousers across the sexes of a taxon were not apparent. Because the preservation of the study skins may have affected both the length and the structural quality of the trousers, I considered this method as appropriate.

Before processing the measurement data I reassessed the sex of each specimen. This was necessary because the sex was omitted on the specimen's label in some cases and questionable in other cases. Sexing was achieved by comparing a combination of two or more parameters (as recommended by Winker (1998)), often wing and tail lengths, that were taken from the specimen in question and other specimens of the same taxon and geographical region. Because most species concerned here exhibit a pronounced reversed sexual dimorphism in body mass (White et al. 1994; see also Table 2.1) and hence may show only limited overlap across the sexes in only a limited number of linear measurements, this method of sexing these birds is accurate.

The data pertaining to 'side feather length' and 'length of the unfeathered portion of the tarsometatarsus' were then processed in three steps. For each taxon I calculated at first the median for each sex. The median was used because the data of the samples were distributed asymmetrically. Second, for the *Falco* species other than *F. peregrinus* (for which, see next paragraph) these medians were adjusted for Grey Falcon male and female median body mass, respectively; for Grey Falcon the aforementioned medians (412 g and 502 g) were used, for the other species the body masses were obtained from the available literature (Table 2.1). Third, the arithmetic average of the medians of the sexes, adjusted for body mass, was computed. The results facilitate the direct comparison of each species with Grey Falcon.

For the subspecies of *F. peregrinus*, measurement data were processed similarly to those above with the exception that the sex-specific medians for side-feather length and unfeathered length of the tarsometatarsus were adjusted for wing length of Grey Falcon rather than body mass. The calculations were based on the sex-specific median wing lengths of the specimens involved, including those of Grey Falcon. This was necessary because the body masses for *F. peregrinus* subspecies are unavailable. In consequence, data from Grey Falcons were independently compared with each of the two groups (i) subspecies of *F. peregrinus* and (ii) the other species of *Falco*.

Both methods of adjusting measurements are biased. They neglect, for example, differences in temperature inertia between species of greater or lesser body mass than Grey Falcon, and species-specific ratio differences of wing-length to linear measurements of other body parts. However, the choices of the taxa and individual specimens *per se*, together with the very small sample sizes, limit *a priori* the precision of the analysis.

Nevertheless, these methods may reveal general patterns and are thus suitable for the purpose of this study.

2.3 Results

Behaviour

Throughout the year adult Grey Falcons keep physical activity levels low, even when they are most active (Table 2.3). This was consistent for the key activities examined, namely flight mode, hunting, and agonistic behaviour, while actively breeding and otherwise (Figure 2.2). For example, when adults left the nest or roost they mostly soared in thermal updrafts (82%, n = 105) rather than flapped their wings; they clearly searched for updrafts after gliding from their perch. They used wing beats only when they failed to detect a

Table 2.3 Observations of key behaviours of adult Grey Falcons, categorized in each case with respect to the intensity with which that behaviour was carried out. 'Bft', wind force according to the Beaufort scale (see text). 'LST', local solar time (see text).

Behaviour	n	Observation frequency	Remark
Flight mode when leaving the site	105	Soaring, very few or no wing-beats: 86 (82%) wing-beating, updraft unavailable: 7 (7%) wing-beating against wind ≥3 Bft: 12 (11%)	All 7 cases of 'updraft unavailable' concern 0624–0727 hr LST
Hunting	18	1 stoop: 14 (78%) (1 successful) 2–3 stoops: 4 (22%) (2 successful) > 3 stoops: nil pounces: nil tail-chases: nil	Gave up after 1–3 stoops
Agonistic behaviour at a nest site while breeding (up to fledging of young)	102	No action [1]: 73 (72%) Active aggression: 29 (28%)	Rarely stooped more than once
Agonistic behaviour at a known or presumed nest site, while associated with fledged young ≤ 12 mo after fledging	31	No action [1]: 23 (74%) Active aggression: 8 (26%)	Often 1 and never more than 2 stoops
Agonistic behaviour while not breeding and not associated with offspring, at a known or presumed former breeding site	16	No action [1]: 10 (62.5%) Active aggression: 6 (37.5%)	5 of the 6 aggressions occurred between mid July and mid October, i.e. the core of the species' breeding season, and involved presumed resident kestrels and hobbies

[1] Even if the intruder was close to the nest the adult Grey Falcon(s) did not take flight, but they sometimes uttered one or more cackling calls or looked at the intruder.

thermal updraft; this was usually the case during the first 1–2 hours after sunrise and also during moderate to strong winds. In almost all cases the landscape inhabited by these birds was flat and orographic updrafts unavailable (e.g., Figure 2.1).

The method of hunting was exclusively stoops, either short steep dives or longer shallow dives interspersed with intermittent wing-beats for acceleration. Most attacks (78%, n = 18) involved a single stoop even if the attack was unsuccessful. Hunting success was 17%.

Adults, while actively breeding, took no physical action in 72% of the cases (n = 102) in which intruders, and these were birds exclusively, approached the vicinity of the nest site. This was independent of whether the nest contained eggs or young. When the adult Grey Falcon(s) attacked the intruder(s) they almost invariably stooped only once at the intruder(s) regardless of whether this deterred the latter. The distance at which intruders were attacked seemed to depend partly on the individual Grey Falcon; some individuals were clearly more aggressive than others. Because intruders were conspicuous at considerable distances in the often flat and treeless surroundings of the nest sites (e.g., Figure 2.1), they were attacked at distances of up to 500 m from the nest, but typically only if they were much closer to the nest. In eight (8%) of these 102 cases in which intruders approached the vicinity of the nest site, the intruder(s) attacked or harassed the breeding Grey Falcons. Even in these cases the adult Grey Falcons took no physical action but responded by evading or ignoring the aggressor.

Of the 96 feeding events, 47 events occurred on six days with $T_{max} \leq 32^{o}C$ and 49 events occurred on 12 days with $T_{max} \geq 34^{o}C$. I used this division because 33ºC appeared to represent the turning point in the thermoregulatory behaviour from heat-seeking to heat-avoiding (Table 2.4). For these two temperature categories (≤ 32ºC and ≥ 34ºC) the distributions of the feeding events over the course of the day were similar (Figure 2.3) and there was no statistical relationship between feeding frequency and maximum daytime temperature (χ^2 (3, n = 96) = 0.740, p = 0.8639). For both temperature categories the feeding distributions show a minimum for the first two hours in the morning, i.e. the coolest part of the day (respectively 11% of 47 and 14% of 49 feeding events), and a peak in the early afternoon (respectively 40% and 33%), the hottest part of the day. The highest number of feeding events in a day involved a family with three newly-fledged young, on a day with $T_{max} = 29^{o}C$. The 13 feeding events occurred between 0804 and 1632 hr LST, and seven of these (54%) were between 1205 and 1434 hr LST. The lowest number of feeding events in a day, two, involved a pair where the female was incubating eggs, on a day with T_{max} = 31ºC; feeding times were 1003 and 1708 hr LST.

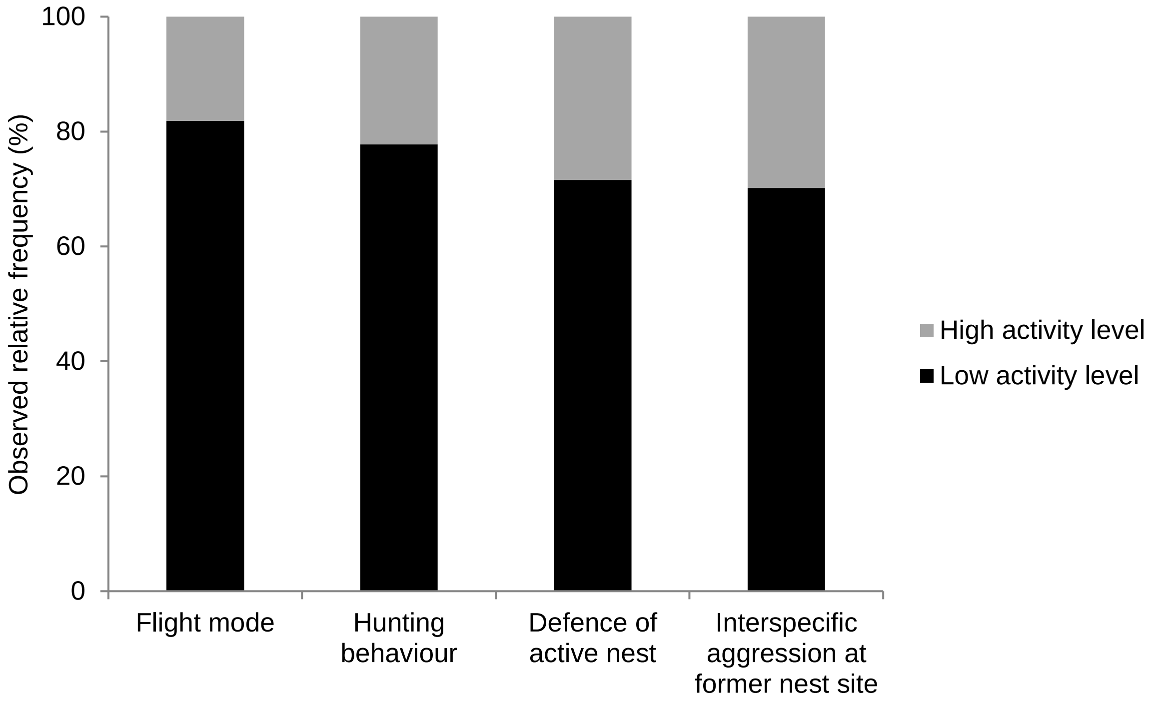

Figure 2.2 Relative frequencies of low and high activity levels of key behaviours of adult Grey Falcons. See text for further details and Table 2.3 for the data on low and high activity levels which are categorized as follows. **Flight mode** (n = 105) ('low activity level', gaining height by means of soaring in a thermal or, rarely, orographic updraft with no more than the occasional wing-beat, followed by directional gliding; 'high activity level', active wing-beating flight, often into the wind, without soaring). **Hunting behaviour** (n = 18) ('low activity level', stooping or pouncing at a target only once; 'high activity level', stooping at a target more often than once, typically two or three times). Incidences of **nest defence** or its absence (n = 102) ('high activity level', taking flight and stooping at the intruder; 'low activity level', remaining perched), shown by breeding adults within about 500 m of the nest site. Incidences of **aggression** or its absence (n = 47) shown toward intruders at known or presumed former breeding sites.

The particular behaviours of Grey Falcons of all ages that were considered to serve thermoregulation are presented in Table 2.4. The most common thermoregulation behaviours were airing and panting. In general, thermoregulatory behaviours were influenced by factors such as exposure to the sun, time since physical activity, and wind force. For example, at 40ºC air temperature and wind of 4 Beaufort, the adults and nestlings in a nest in full sun were not panting, but an adult pair panted at 41ºC in part-shade at a 2-Beaufort wind. Adults were never seen shading their nestlings, and this involved 42 nests observed over a total of 1010.25 hours. For example, at a nest in full sun, at 42ºC and intense solar radiation (at 1353 hr LST) both adults were perched near the nest but did not shade their downy young aged about 14–16 days. The high thermal tolerance of the young is further illustrated by the observation of two approximately 10-day-old nestlings left alone by their parents for an entire night (Schoenjahn 2011c) when the minimum temperature was 13ºC and the wind a light breeze of 1–2 Beaufort.

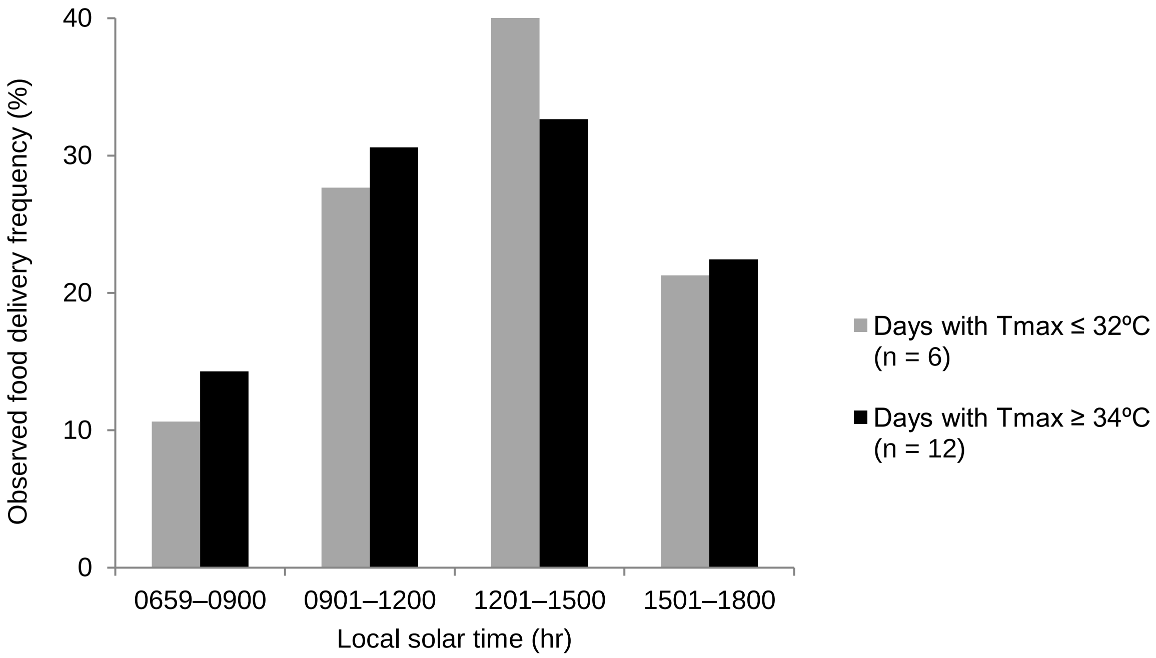

Figure 2.3 Relative frequencies of observed feeding events (n = 96) at nest sites while nests contained eggs or nestlings, arranged by colder (T_{max} ≤ 32ºC) and warmer days (T_{max} ≥ 34ºC) in four daytime periods. Data were collected during 18 full days (n = 18), i.e. from sunrise to sunset, at 12 different nest sites during August to October of the years 2007–2016. Note that on any given day additional feeding events may have occurred elsewhere or otherwise unnoticed by the observer.

Table 2.4 Incidental observations of presumed thermoregulatory behaviour of individual Grey Falcons of all ages. 'Nestling', nestling of any age in a nest while both parents were absent or perched away from the nest; 'LST', local solar time (see text); 'n', observation frequency; 'Bft', wind force in Beaufort (see text); '–', this age group could not be assessed because the relevant situation was not encountered; 'No such behaviour observed', birds of this age group were observed for meaningful lengths of time at the temperature range indicated but behaviours that could have been interpreted as serving thermoregulation were not recorded.

Temperature range	Adult and juvenile	Nestling
≤ 20ºC	After a cold night (≤ 3ºC), a non-breeding pair roosted in full sun until 0935 hr LST, then left for the day (n = 2)	–
~30ºC	Moved into sun (wind 3 Bft) (n = 1) Perched in full sun (wind 1–2 Bft) (n = 1)	No thermoregulatory behaviour observed (in full sun) (n = 2)
34–36ºC	Tracked shade intermittently (wind 1–2 Bft) (n = 1) Panting (wind 1–2 Bft) (n = 2) Airing and on/off panting (n = 1) After having returned to nest/roost from hunting, airing and (for 2 min) panting (intense solar radiation) (n = 1)	Airing and on/off panting (in full sun, wind 1–2 Bft) (n = 3)
37–39ºC	Tracking shade while feeding (n = 1) Panting (n = 1) Airing (n = 1)	Airing and on/off panting (near full sun, wind 1–3 Bft) (n = 3)
40–43ºC	No thermoregulatory behaviour observed (in full sun, wind 3–4 Bft) (n = 4) Panting (wind 2 Bft) (n = 3) Panting on/off (wind 2 Bft) (n = 1)	No thermoregulatory behaviour observed (in full sun, wind 3–4 Bft) (n = 2) Downy young panting (42ºC, in full sun, wind 1–2 Bft) (n = 4)

Anatomical characteristics

The results of the analyses of morphometrical data of 11 species of *Falco*, including *F. hypoleucos*, are presented in Table 2.5. These results, however, reveal no general patterns. Further, the data do not lend themselves to statistical analyses because assigning values for climatic parameters to a taxon is not straightforward and therefore not attempted here. Reasons are that (i) most taxa involved breed in more than one climate zone (e.g., the Black Falcon breeds in arid-hot and humid-hot environments), (ii) some taxa migrate and thus regularly spend considerable periods in each of two or more climate zones (e.g., Sooty Falcons breed in the arid-hot climate zone and migrate to Madagascar which has a humid climate), and (iii) parts of the population of some taxa use more climate zones than other parts of the same taxon because they differ in their movement ecology from another (e.g., the Red-headed Falcon is partly nomadic and partly sedentary (Appendix 2)).

Some broad generalizations can be made, however. For each of the two groups analysed, the taxon that is associated with the coldest climate has the most complete feathering of the tarsometatarsus; these are the largely sedentary Gyrfalcon *F. rusticolus* and the highly migratory North American Tundra Peregrine *F. peregrinus tundrius*. The specimens of Gyrfalcon have, in addition, the longest and thickest trousers of all taxa examined. The species that has the shortest side-feathers, by far, among the species investigated in Table 2.5(a), lives in the most extreme humid-hot environment, namely the Orange-breasted Falcon *F. deiroleucus*. The same cannot be said from the *F. peregrinus* subspecies (Table 2.5b). Individuals of the form *ernesti* have comparatively long side feathers but live exclusively in humid-hot environments. Grey Falcons, living in arid-hot environments, also have comparatively long side feathers (Table 2.5a). Only the specimens of the two strictly migratory species, Eleonora’s Falcon *F. eleonorae* and Sooty Falcon *F. concolor*, have relatively longer side feathers, and these species are not particularly close to the Grey Falcon phylogenetically (Figure 1.2). The Grey Falcon has long side feathers compared to all subspecies of the *F. peregrinus* group (Table 2.5b). In regard to the adjusted unfeathered length of the tarsometatarsus of the taxa examined (range 20.7–37.6 mm for the body mass-adjusted group, range 29.8–37.7 mm for the wing length-adjusted group), the Grey Falcon does not stand out (28.1 mm), and the same is true in regard to the quality of the trousers.

Table 2.5 Morphological data (medians, sexes combined) taken from museum specimens of various species of the genus *Falco*, and their corresponding climate classes (see Peel et al. 2007). See text (Methods) for way in which data were computed. 'n', sample size; 'Tarsus', tarsometatarsus. 'Trousers', crural flags (see text). For details of specimens see Appendix 3. Highlight indicates Grey Falcon. (a) Ten species of the genus *Falco* including *F. hypoleucos*, but excluding *F. peregrinus*. 'br' and 'nb' denote that the climate classes pertain to the breeding and non-breeding areas of this strictly migratory species rather than to the sites where the specimens were collected; 'adj.', adjusted for Grey Falcon body mass to allow comparison; see text for details. (b) Thirteen subspecies of *Falco peregrinus* (subspecies delimitations follow White et al. 2013). 'adj.', adjusted for Grey Falcon wing length. All wing lengths concerned were taken from the specimens involved in this study. See text for details.

(a) *Falco* species

Species of *Falco*	n	Climate Classes of specimen locations	Climate description	Side feather length (adj.) (mm)	Unfeathered portion of tarsus (%)	Unfeathered length of tars. (adj.) (mm)	Trousers
chicquera	6	BWh, BSh, Aw	Arid–hot, Tropical	76 (n = 5)	79 (n = 6)	37.6	Cover 1/3 to 1/2 of tarsus
eleonorae	4	br: Csa, Csb nb: BWh, BSh, A	Temperate–warm or hot summer Arid–hot, Tropical	86 (n = 4)	71 (n = 3)	27.3	Most extend to about the base of the toes; bushy but not thick
concolor	4	br: BWh nb: Cfa, Cfb, A	Arid–hot Temperate–warm or hot summer, Tropical	90 (n = 4)	79 (n = 4)	32.0	Variable, cover 1/2 or more of tarsus, some extend beyond base of toes; bushy or thick
deiroleucus	4	Cfb, A	Temperate–warm summer, Tropical	68 (n = 4)	71 (n = 4)	27.2	Reach almost to base of toes
hypoleucos	10	BWh, BSh	Arid–hot	82 (n = 9)	66 (n = 9)	28.1	Reach base of toes; broad, thick
subniger	4	BWh, BSh, A	Arid–hot, Tropical	78 (n = 4)	86 (n = 4)	35.2	Reach base of toes; thick
biarmicus	4	Cwa, BWh	Temperate–hot summer, Arid–hot	74 (n = 4)	71 (n = 4)	32.3	Reach almost to base of toes; massive, bushy and thick
jugger	5	BSh	Arid–hot	76 (n = 5)	70 (n = 5)	29.1	Most reach base of toes, some slightly shorter
rusticolus	12	E	Polar	75 (n = 12)	48 (n = 12)	20.7	Extend beyond base of toes; very thick
mexicanus	6	Dfb, BWk, BSk	Cold–warm summer, Arid–cold	76 (n = 5)	65 (n = 6)	29.4	Variable, cover 1/3 to 4/5 of tarsus

[continued]

Table 2.5 (cont.)

(b) Falco peregrinus subspecies

Subspecies of *Falco peregrinus*	n	Climate Classes of specimen locations	Climate description	Side feather length (adj.), mm	Unfeathered portion of tarsus, %	Unfeathered length of tars. (adj.), mm	Trousers
anatum	4	Dfb, BSk	Cold–warm summer, Arid–cold	68 (n = 4)	76 (n = 4)	32.9	Cover 1/3 to 1/2 of tarsus
babylonicus	2	BWh	Arid–hot	78 (n = 2)	79 (n = 2)	36.2	Cover ~1/2 of tarsus, rather thin
cassini	3	BSk, C, E	Arid-cold, Temperate, Polar	74 (n = 3)	77 (n = 3)	33.1	Cover ~4/5 of tarsus, thick
ernesti	5	A	Tropical	80 (n = 5)	75 (n = 5)	35.1	Cover ~4/5 of tarsus, variable, some are bushy and thick
macropus	4	BSk, Cfb	Arid-cold, Temperate–warm summer	80 (n = 3)	80 (n = 3)	35.8	Cover ~4/5 of tarsus, lateral only, bushy
minor incl. *perconfuscus*	6 [1]	Csb, Cwb, BWh, A	Temperate–warm summer, Arid–hot, Tropical	78 (n = 6) [1]	78 (n = 6) [1]	34.2 [1]	Cover ~1/2 of tarsus, narrow, lateral only, bushy
nesiotes	2 [1]	A	Tropical	73 (n = 2) [1]	75 (n = 2) [1]	34.1 [1]	Cover ~1/2 of tarsus, broad and thick
pealei	4	C, D	Temperate, Cold	72 (n = 4)	72 (n = 4)	32.0	Cover ~4/5 of tarsus, anterior and lateral, fairly thick
pelegrinoides incl. *arabicus*	5	BWk, BWh, BSh, Aw	Arid-cold and hot, Tropical–savannah	79 (n = 5)	82 (n = 4)	33.9	Variable, cover from 3/4 to 4/4 of tarsus, thick at anterior
peregrinator	5	Cfa, BSh, Aw	Temperate–hot summer, Arid–hot, Tropical–savannah	82 (n = 5)	79 (n = 4)	37.7	India (n = 3): 1/2–3/5, lateral only China (n = 2): 4/5, quite bushy
peregrinus	4	Cfb	Temperate–warm summer	73 (n = 4)	82 (n = 4)	35.7	Reach base of toes
radama	3	A	Tropical	75 (n = 3)	71 (n = 3)	32.2	Cover 2/3 of tarsus – extend beyond base of toes, slim, thick
tundrius	4	E, Dfc	Polar, Cold–cold summer	69 (n = 4)	70 (n = 4)	29.8	Cover ~4/5 of tarsus, slim to broad, thick

[1] The sample contained only male specimens.

2.4 Discussion

The overarching aspect of Grey Falcon behaviour that I have documented in the current research is that throughout the year these birds keep activity levels low. This pattern is particularly obvious in comparison to the Peregrine Falcon, a well-studied species that also specializes on avian prey (Table 2.6). Grey Falcons are far less active than Peregrines in every aspect examined, despite these species both being active bird hunters. This finding, together with the extreme extent of the differences, suggests that the low activity levels in the Grey Falcon are unlikely a coincidence but rather a necessity for their survival in their extremely hot, arid, low productivity environment. To explain the year-round low activity levels I examine key behaviours of the Grey Falcon in the following sections to assess how they may be related to its permanent residence in the hot arid zone of Australia.

Dietary and climatic specializations

The Grey Falcon stands out among its congeners worldwide in two fundamental ecological aspects. These are its specializations in diet and climate (Appendix 1). First, the Grey Falcon's diet is the most restricted of any species in the genus *Falco*, consisting virtually exclusively of birds throughout the year and independent of age (Schoenjahn 2013). Even acknowledged bird specialist predators like the Peregrine Falcon and Taita Falcon *F. fasciinucha* feed in other ways. These alternative foraging strategies include kleptoparasitism (Peregrine Falcon; Zuberogoitia et al. (2013)), and the inclusion of substantial proportions of alternative prey into their diet (Peregrine Falcon: lemmings (Bradley and Oliphant 1991), voles (Cade 1982), bats (Clunie 1972, Jenkins 1995, Stevens et al. 2009), and large insects (Stevens et al. 2009); Taita Falcon: insects (Hunter et al. 1979, Hartley et al. 1993). Of interest is the extent to which these specialists include prey other than birds in their diet. For example, the prey biomass of the Peregrine Falcons studied by Bradley and Oliphant (1991) comprised as much as one third mammalian prey, even in non-peak rodent years.

Second, the Grey Falcon is the only *Falco* species that is restricted to the arid climate zone. Other *Falco* species that have a reputation for their association with the arid zone, such as the Laggar Falcon and Prairie Falcon (White et al. 1994), are regularly found in other climate zones. Even if some individuals of the latter (and perhaps some other species) do persist exclusively in the arid zone, the entire population of the species does not. Furthermore, the Grey Falcon is restricted to an area with some of the highest average annual temperatures globally: Australia's arid and semi-arid zone (Kottek et al.

2006, Schoenjahn 2013). This zone is characterized by extreme climatic events that are unpredictable in occurrence, duration, and severity (Morton et al. 2011). These events include droughts lasting from a few months to several years (e.g., 'Federation Drought', 1895–1903; 'Millennium Drought', 2001–2009 (Liddy et al. 2014)), heat waves with daytime temperatures exceeding 50ºC, strong hot winds (while monitoring nests I experienced repeatedly near gale force winds at temperatures above 35ºC), sand- and dust storms, deluges of rain (e.g., Tennant Creek in central Australia received 323 mm between 16 and 24 Jan. 2009, and 90.8 mm on 18 Jan. alone; in that general area Grey Falcons bred in 2008), and, in lower latitudes, tropical cyclones.

Table 2.6 Qualitative comparison of key year-round-behaviours of adult Grey Falcons (this study, see text) with those of adult Peregrine Falcons. The references relate to the latter species.

Behaviour	Adult Grey Falcons	Adult Peregrine Falcons	Reference
Flight mode	Predominantly soar in thermals, rarely flap	Mostly restricted to gliding and flapping, relatively poor users of thermals	Jenkins (1995)
		Wing-beating flights may exceed 2 hr	Cochran and Applegate (1986)
Hunting methods	Stoop, never tail-chase prey	Often tail-chase prey	Sherrod (1983)
Hunting perseverance	Give up after 1–3 stoops	'Chases can last many minutes'	Cade (1982, p. 61)
Nest defence	Passive in most incidences	Vigorously defend nest and young	e.g., Herbert and Herbert (1965)
	Often 1 stoop only	≥ 15 stoops in 4 min	Sansom (1990)
	Physical contact not recorded	Defence may lead to death of either opponent	Herbert and Herbert (1965) Garcia (1978)

Hunting activities

The temporal distribution of feeding events at nest sites each day show that adults are active throughout the day. The relatively low feeding frequency in the morning coincides with the observation that these birds favour soaring in thermals over wing-beating flight, and thermals are often unavailable during the first hours of the day (Table 2.3). Providing food for the whole family requires considerable hunting activity from the adults, and in most species of *Falco* it is the male who provides the bulk of the food (Cade 1982). Of note, Grey Falcons are known to raise up to four young to at least fledging age (Schoenjahn, pers. obs.), in line with expectations for all other species of *Falco*; siblicide is unknown among this group and all hatchlings may fledge (Cade 1982). The food-providing effort is reflected in the high number of 13 feeding events (each comprising an individual capture) recorded in a day, but only partly so.

To appreciate the full extent of the hunting effort one has to consider these birds' hunting success. The hunting success for this study was 17%, i.e. one in six hunts, which is within expectations for bird-hunting raptors (Curio 1976). Hunting success of falcons that specialize on bird prey varies considerably and may at times be even lower than 17% (summarized by Cade (1982)). For example, a Merlin *F. columbarius* hunting shorebirds had a success rate of 12.8% in 343 hunts, i.e. one in eight hunts (Page and Whiteacre 1975). Evidently, the combined number of successful and unsuccessful hunts is a multiple of the number of feedings observed. A considerable proportion of the hunting activity of Grey Falcons clearly occurs during the warmer parts of the day. Indeed, the 13 feeding events mentioned above were spread across 8.5 hours and more than half of them were during the hottest part of the day. During these times, the thermoregulatory capacity of the hunting falcons may be challenged further by the behaviour of their bird prey, which is difficult to pursue *per se*. Passerine and other prey species are reported to retreat to the shade and become less active as the day gets hotter (Dawson and Schmidt-Nielsen 1964, Schodde 1982), which may cause additional and prolonged physical effort, and hence increased endogenous heat production.

Thermoregulatory aspects

Morphologically, Grey Falcons appear to possess no obvious characteristics that would predispose them to desert living. For example, the Grey Falcons' flexible long side feathers may help heat dissipation when the air temperature is below skin temperature. However, other *Falco* species that live in hot environments have comparatively short side feathers, for example the Lanner Falcon (see Tables 2.5 and 2.7). Similarly, the Grey Falcons' long trousers may provide shade to the unfeathered parts of the tarsometatarsi when the birds are perched, but the Red-headed Falcon *F. chicquera* also lives in hot environments and has particularly short trousers. Standing out among the results presented in Table 2.5 is that the taxa that live in the coldest climates have the most complete foot feathering. These results are in line with a comprehensive study by Kelso and Kelso (1936) on foot feathering of American owls. In each climate zone owl species with foot feathering of more than one density-type were found, but extremely dense foot feathering was associated with extreme cold climate.

The heat dissipation behaviours of adult Grey Falcon, such as airing and panting, did not seem exceptional, but dedicated physiological tests would be the only way in which this could be quantified, although such tests also have their difficulties. To illustrate, Grey Falcon adults started to pant at air temperatures of 34–35ºC whereas American Kestrels *F. sparverius* did so at 42ºC in an experiment (Bartholomew and Cade 1957). However, such comparisons are inevitably impeded by the design of laboratory tests because they almost invariably lack influences such as solar and secondary radiation, as well as wind (examples are Dawson (1954), McKechnie et al. (2016)), and some even impose temperature regimes that deviate greatly from natural cycles (e.g., the test conducted by Bartholomew and Cade (1957)). Nevertheless, my evidence suggests that the Grey Falcon has heat dissipation capacities similar to those found in other desert-living birds (e.g., Dawson 1954, Williams 1999).

Grey Falcon young are remarkable in their evident tolerance of a wide range of temperatures and heat loads from an early age. At 14–16 days, downy young were exposed, in a nest in full sun, to air temperatures of 42ºC and high solar radiation (Table 2.4). Even 10-day-old young spent a 13ºC night without a brooding parent. By contrast, young of the Peregrine Falcon were brooded during cold weather until about 21 d old (Enderson et al. 1972, Hovis et al. 1985). It may be that Grey Falcons are more tolerant to hyperthermia than to hypothermia, or that they acquire thermoregulation during hot weather earlier than thermoregulation during cold weather. These may, however, be characteristics that are common to birds in general, including those that live in areas other than arid-hot deserts. Further physiological investigation of this situation appears warranted.

The finding that Grey Falcon adults do not ‘shade’ their young was unexpected. Shading is the behaviour of an adult bird when it perches on or near the nest rim with its back to the sun and spreads its wings to provide shade for the nestlings. Many species of birds, including raptors, shade their nestlings to prevent hyperthermia, and the benefits and costs of the behaviour have been studied in detail (Poole 1979, Palmer et al. 2001, Lloyd and Martin 2004, González et al. 2006, Tieleman et al. 2008). Given the Grey Falcon’s restriction to hot environments, the absence of shading seems at first surprising. The young tolerate, however, extreme heat loads at a comparatively early age. This frees both parents early in the life of the nestlings to both go hunting and thus share the increasing food demand of the growing young at a time when the days get hotter with the approach of summer. It thus appears that the early heat tolerance of the young helps the adults to minimize their heat gains from the environment, which is of particular importance at times when the metabolic heat production of the adults (from physical activities) and external heat loads are increasing.

2.5 Conclusion

Grey Falcons live entirely in one of the hottest arid environments of the world, and rely exclusively on one of the most demanding foraging methods, hunting birds. The physical demand of these hunts has the potential to substantially increase the falcons' metabolic rate and thus endogenous heat production (Baldwin and Kendeigh 1932, Bartholomew and Dawson 1954). When the adult birds hunt for their growing young, with up to four young at a time, they are exposed to high air temperatures and intense solar radiation for considerable periods of each day. These two factors were suggested, for other avian species that live in hot environments, to be the main cause of heat stress (Bryant 1983). Grey Falcons appear to lack, in line with most other birds, particular morphological or physiological characteristics that would allow them to cope with heat better than other birds do, with the possible exception of the high thermal tolerance of the chicks. The pathway that is left for Grey Falcons to respond to the challenges of desert living is behavioural. They keep physical exertion and thus activity levels low in each aspect of their lives and through each stage of their lives. This behaviour pertains to the individuals of the species consistently and independently of where they are found and the time or season of the year. It appears, therefore, that this behaviour is an adaptation, i.e. a feature that promotes the spread of an individual's genes to future generations and was evolved for its current role by selection over an evolutionary relevant period (*sensu* Gould and Vrba 1982).

The survival of Grey Falcons appears to depend on a fine balance between gaining heat from the environment and their own metabolism during physical activity, and minimising endogenous heat gains by keeping activity levels low. To achieve this balance Grey Falcons presumably take full advantage of their physiological characteristics, which they share with most bird species. It is likely that the low humidity of their environment plays an import role in this balance because moisture in the air hampers evaporative cooling and helps to conduct heat; higher air humidity may thus tip the balance. This may explain the Grey Falcon’s absolute restriction to the arid and semi-arid zone.

Chapter 3

Staying cool is key – the unparalleled extension of juvenile dependence in an arid-zone endotherm, the Grey Falcon

3.1 Introduction

The young of almost all endothermic species depend on their parents for protection whilst they learn to forage or hunt for themselves. Their thermoregulatory and other metabolic requirements necessitate a dependable and regular food supply. In most species of birds, including raptors, the young depend on their parents for the provisioning of food for some time after fledging (Lack 1954, Fogden 1972, Burger 1980, Heinsohn 1991). During this period young birds learn skills from their parents that are necessary for their subsequent nutritional independence. Skills include the localization and recognition of foraging areas and suitable food or prey, foraging or hunting behaviour and food handling (Nelson 1971, O’Connor 1984, Varland and Klaas 1991, López-López et al. 2014). Rapid learning in a short time can be expected to be favoured by natural selection because it reduces the period of vulnerability, and cases of comparatively slow juvenile development have, therefore, attracted scientific attention, for example in primates (reviewed by Jones (2011)). In birds, cases of relatively long juvenile dependence in a species have usually been attributed to the juveniles requiring a long time to attain foraging independence (e.g., Heinsohn 1991, Hunt et al. 2012). The difficulties may stem from having to learn foraging techniques that require extended learning periods, including tool use (e.g., New Caledonian Crow *Corvus moneduloides* (Hunt et al. 2012)) or the location of scarce or alternative food sources (e.g., frigatebirds (Burger 1980)).

In diurnal raptors (Falconiformes), dependence periods of young range from a few days up to 4 wk for small falcons and sparrowhawks, 4–6 wk for large falcons (Table 3.1), 5–12 wk for buzzards and kites, and up to about 6 mo for some large eagles and vultures (see Newton (1979) for review). Some of the largest raptors even have post-fledging dependence periods longer than 6 mo. Their reproductive cycles extend more than 12 mo, so they breed only every second or third year. Examples include the Andean Condor

Vultur gryphus (Brown and Amadon 1989) and Harpy Eagle *Harpia harpyja*, the latter probably having the longest post-fledging period (around 1.5 yr) and longest breeding cycle (more than 2 yr) of any raptor (Muñiz-López et al. 2012, p. 510, Aguiar-Silva and Sanaiotti 2013).

Table 3.1 Post-fledging periods of some species of *Falco* as reviewed by Newton (1979), unless indicated otherwise. Body mass (sexes combined) according to White et al. (1994), unless indicated otherwise.

Species of *Falco*	Common name	Post-fledging period (wk)	Body mass (g)
naumanni	Lesser Kestrel	<1 [1]	90–208
vespertinus	Red-footed Falcon	1–3	130–197
subbuteo	Eurasian Hobby	2–3	131–340
sparverius	American Kestrel	3	80–165
tinnunculus	Common Kestrel	3.5–4	136–314
rusticolus	Gyrfalcon	4	961–2100
berigora	Brown Falcon	1–6	405–860 [2,3]
biarmicus	Lanner Falcon	4–6	500–900
cherrug	Saker Falcon	4–6	730–1300
peregrinus	Peregrine Falcon	5–6	550–1500
subsp. *macropus* *		10+ [4]	505–960 [2,3]
subniger *	Black Falcon	8 [5]	510–1000

* Endemic to Australia.
[1] Bustamante and Negro (1994).
[2] Marchant and Higgins (1993).
[3] Live adult birds (banding data).
[4] Sherrod (1983) (sample size n = 1).
[5] Charley et al. (2014).

The juvenile dependence period of raptors has been studied from several perspectives, including whether the parents or the young determine the end of this period (e.g., Brown 1966, Alonso et al. 1987, Mínguez et al. 2001, Arroyo et al. 2002), whether the young hunt for themselves during this period (reviewed by Newton (1979)), and the influence of weather and prey availability (e.g., Arroyo et al. 2002, Walls et al. 2005, Balbontín and Ferrer 2009). Also, the comparative duration of the juvenile dependence period across similar species has received consideration (e.g., Johnson 1986, Donázar and Ceballos 1990).

The Grey Falcon *Falco hypoleucos* is a little studied, endemic Australian raptor and is considered one of the five rarest of all *Falco* species (Schoenjahn 2013). It has an estimated population of <1000 mature individuals (Garnett et al. 2011; Schoenjahn 2011a;

BirdLife International 2012) that are distributed sparsely over Australia’s arid and semi-arid zone (Schoenjahn 2013), an area of about 5 million km^2 (Australian Museum 2002; Pavey and Nano 2006) or 70% of the Australian mainland. The Grey Falcon is a medium-sized falcon with a median body mass of adults captured from the wild of 412 g (n = 7; range 339–448 g) for males, and 502 g (n = 9; range 486–582 g) for females (Schoenjahn (2011b) and Schoenjahn, unpublished data). Grey Falcons of all ages feed almost exclusively on birds (Schoenjahn 2013).

The available literature on the Grey Falcon, which is largely anecdotal (only two publications were listed for this species by the Web of Science, http://apps.webofknowledge.com/; verified 10 Aug. 2017), hints a behaviour that would be, if shown to be characteristic for the Grey Falcon, unique among members of the genus *Falco*, unique indeed among raptors of similar size. Juvenile Grey Falcons and their parents have been reported being closely associated with one another many months after fledging, i.e. at a time when the juveniles in all other raptors of comparable size are fully independent and no longer closely associated with their parents (Table 1.2). However, this behaviour of the Grey Falcons has never been quantified and the nature of the interaction has never been investigated. An explanation for the behaviour has been proposed by Olsen (1995, p. 167): ‘it may be an adaptation to harsh life in the arid inland’, but without explication or justification. Indeed, the species is restricted to areas classified as ‘hot desert’ and ‘hot savannah’ (Schoenjahn 2013), the hottest climate zones recognized by the Köppen-Geiger Climate Classification (Peel et al. 2007). These arid and semi-arid environments are governed predominantly by precipitation, and this is unpredictable in occurrence, duration and productiveness (Noy-Meir 1973), causing unpredictable episodes of boom and bust (Chapter 1).

I investigate the occurrence and characteristics of delayed juvenile independence in this chapter. First, I collate information on the extent of the dependency period in this species to test whether the juvenile dependence in Grey Falcons is as extended as the available anecdotal reports seem to suggest. I then investigate (i) how parents support their young during that period and the extent to which they do this, and (ii) the development of key survival skills in juveniles. To give perspective to these behaviours recorded in Grey Falcons I compare them (from literature sources) with those of other *Falco* species. I found that Grey Falcons differ significantly from all other falcons and similar-sized raptors, with regard to the duration during which a family stays together and the time it takes to develop survival skills in juveniles. These findings strongly suggest that an ecological explanation for these two behaviours exists. Because the ‘harsh’, i.e. extreme and unpredictable, climate that typifies the species’ environment has already been suggested to be a key factor in explaining the species’ scarcity (Schoenjahn 2013), I then consider whether the extended juvenile dependence and its associated features could indeed be explained as adaptations to the Grey Falcon’s environment.

3.2 Methods

The general methods and study area have been described by Schoenjahn (2013). Data were collected between July 2003 and November 2016. Search effort was not consistent and not systematic because of the species’ extremely low density and massive geographic distribution, and because the species may be nomadic to some extent (Chapter 1). The difficulties of the fieldwork may be illustrated by the circumstance that in the 2015 breeding season, for example, I travelled 18540 km and found only six breeding pairs, with the greatest straight distance between two nests being 2660 km (Appendix 4).

For data collection concerning family groups staying together for extended periods I relied on my own observations (n = 17), and the unpublished reports by others (n = 14) that had been supported by photographic evidence or conclusive descriptions of field marks consistent with those provided by Schoenjahn (2010b). Only those observations made between 15 Mar. and 31 Oct. (of 2003–2016) are included, to cover the period 5–12 mo after fledging of the young, an age at which the young of all other raptors of similar size to Grey Falcon have long left their parents, including all *Falco* species studied in this respect (Table 3.1). The threshold of five months after fledging leaves no room for misinterpretation of the data.

Each family record (n = 31) contained at least the following information: confirmed identification, date, location, and number of birds. Sex and age were assessed through direct observation in the field or from photographs. Distinguishing young Grey Falcons from adults is straightforward for several months after fledging (Schoenjahn 2010b). Juveniles at the age of about one year (“yearlings”) may be recognized by remnants of juvenile plumage and their bare parts not being as bright orange-yellow as in adults (Schoenjahn (2010b) and Schoenjahn, pers. obs.). A group of Grey Falcons was considered to be a family group if it consisted of two or more individuals, with at least one juvenile and one adult that were clearly associated with one another, for example roosting closely together on the same tree or artificial structure (e.g., telecommunication repeater tower (Figure 2.1)).

Observations of groups within 200 km of each other at different times of the same year were considered to have a high enough probability of representing repeat observations on the same family, so only the latest record in the year was included in the data set and analysis. The threshold of 200 km was chosen on the basis of the movements of a satellite-tracked Grey Falcon in its first year that did not move more than 155 km from its natal site during April–October 2014 (Chapter 4). Therefore I am confident that groups were not sampled more than once.

The interactions of the juveniles (5–12 mo after fledging) with their parents, and also the key motor skills of the juveniles, from 16 family groups (one of the 17 families mentioned above remained perched during the observation period and could not be assessed) were recorded exclusively by me, thus ensuring that the age, sex, and behaviours of the birds involved were determined consistently. A juvenile was presumed to be night-roosting together with its parent(s) when the birds were observed roosting closely together at around sunset or sunrise. This definition was used because these birds remain, until sunrise, where they settled the previous evening (Schoenjahn, pers. obs.). Food-soliciting was recorded if juveniles begged (vocally) or harassed (behaviourally) a parent. Motor skills of juveniles were assessed by comparing these to those of adults. Skills included flying skills (e.g., avoiding collision with obstacles in the flight path), selecting a suitable perch (e.g., a horizontal perch), precision landing and perching successfully and securely on the perch, food handling and food passing. A total of 380 hours (median 20.75 hr, range 1.25–78.0 hr) was spent observing young-parent interactions in the 16 family groups.

The term ‘breeding pair’ is used for a pair that is assumed capable of breeding even though the pair may not breed in a given year. ‘Fledging’ is defined as the moment when the fully feathered young bird voluntarily leaves the nest for the first time, typically with a short flight (after Steenhof and Newton 2007, p. 184). This is how most researchers understand the term (e.g., Burger 1980), including those working on raptors (Newton 1979, Brown and Amadon 1989). The associated terms ‘post-fledging period’ (e.g., Newton 1979, Arroyo et al. 2002, Steenhof and Newton 2007) and ‘post-fledging dependence period’ (e.g., Bustamante 1994, Rahman et al. 2015) are avoided because they are not used consistently in the literature (Steenhof and Newton 2007). Because juvenile Grey Falcons, even at an unusually advanced age, may still be associated closely with their parents and at least partly depend on them, the term ‘extended juvenile dependence’ is used to describe this suite of behaviours.

3.3 Results

Family groups

Thirty one independent family groups were recorded in the period 2007–2016 (Table 3.2). Fourteen (45%) of the observations were in the months September and October (Figure 3.1), the core of the breeding period (see below), which shows that the period of dependence even overlaps with the following breeding season of the parents. From observations at active Grey Falcon nests in 2007–2016, the median of the estimated fledging dates was 12 Oct. (n = 44, range 73 d, 16 Sep.–27 Nov.). Median inferred hatching date was 21–24 Aug. These dates were estimated on the basis of the hatching and nestling periods being 35 d and 49–52 d, respectively (Chapter 1).

The highest number of family groups recorded in a year was eight, in 2012 (Figure 3.2). Of these, two families were seen at sites where breeding was recorded in 2011, whereas two families were seen at sites where this was not the case. Whether breeding occurred in 2011 at the remaining four sites is not known because they were not monitored in that year. Five of the eight family groups were found in October, the peak of the breeding season, i.e. 12 mo after these juveniles had fledged, and all within a circle of 600 km diameter, in Queensland. None of the adults of these five families bred in 2012.

Observations (n = 8) that involved juvenile Grey Falcons 6–12 mo after fledging but no adults are listed in Table 3.3. Note that in all eight cases adults were not searched for and may have been overlooked.

That pairs are capable of breeding in successive years, and partners may stay together for more than one breeding event, was evidenced by the observation of a pair of Grey Falcons in which both individuals were colour-banded in 2010 while breeding at a site in Queensland. The same pair bred successfully again in 2011 at the same nest. No pairs of Grey Falcons were found breeding more than once in a year and they did not breed every season.

Table 3.2 Records of different groups (see text) of two or more individuals of Grey Falcon observed together between 15 Mar. and 31 Oct. 2007–2016 (n = 31). Groups consisted of one or two adults (ad.) in close company of one or more juveniles (juv.). It was not always possible to determine age and sex of all birds in a group. Abbreviations in the "Comment" column as follows: 'NS', nesting site in the year shown; 'nl.', nestling(s); 'fl.', fledgling(s) (number of nestlings and fledglings provided if known); '~', the record was made in the vicinity of a known nesting site; 'No', the site was not a nesting site in the year before the family group was observed.

	Month	Day	Year	State *	No. of birds	Age, sex	Comment
1	Mar.	23	2015	Qld	2	1 ad. ♀, 1 juv. ♂	
2		27	2015	Qld	2	1 ad. ♀, 1 juv. ♂	
3		31	2008	Qld	4	2 ad., 2 juv.	
4	Apr.	4	2014	WA	3	2 ad., 1 juv. ♀	~NS 2013 (2 nl.)
5		mid	2013	Qld	4	2 ad., 2 juv.	
6		17	2011	NSW	2	1 ad., 1 juv.	
7		26	2014	NSW	3	2 ad., 1 juv.	
8	May	10	2016	WA	4	2 ad., 2 juv.	~NS 2015
9		13	2013	NSW	5	2 ad., 3 juv.	
10		15	2008	WA	3	2 ad., 1 juv.	NS 2007 (2 fl.) [1]
11		19	2013	WA	3	1 ad., 1 juv.	
12		late	2012	Qld	4	2 ad., 2 juv.	
13	June	early	2014	NT	3	2 ad., 1 juv.	
14		2	2008	WA	4	2 ad., 2 juv.	
15	July	6	2008	Qld	3	2 ad., 1 juv.	
16		10	2012	NSW	3	1 ad., 2 juv.	
17	Aug.	9	2008	WA	2	1 ad. ♀, 1 juv. ♂	
18	Sep.	11	2011	Qld	3	2 ad., 1 juv.	NS 2010 (2 fl.) [2]
19		19	2009	NT	2	1 ad. ♀, 1 juv. ♂	NS 2008 (1 nl.)
20		28	2008	Qld	2	1 ad. ♀, 1 juv. ♂	
21		29	2012	NT	2	1 ad. ♀, 1 juv. ♂	
22	Oct.	1	2015	NT	3	2 ad., 1 juv. ♀	see [3]
23		2	2012	Qld	3	1 ad., 1 juv.	
24		2	2016	Qld	4	2 ad., 2 juv.	NS 2015 (2 nl.) [3]
25		4	2012	Qld	3	2 ad., 1 juv.	NS 2011 (4 fl.)
26		4	2015	SA	3	2 ad., 1 juv. ♀	see [3], [4]
27		7	2007	Qld	3	2 ad., 1 juv.	
28		7	2012	Qld	4	2 ad., 2 juv.	No; see [5]
29		12	2012	Qld	2	1 ad., 1 juv.	NS 2011(? nl.)
30		17	2012	Qld	3	2 ad., 1 juv.	No; see [6]
31		31 [7]	2009	Qld	3	1 ad., 2 juv.	NS 2008 (2 fl.)

* The Australian States and Territories mentioned are 'NSW', New South Wales; 'NT', Northern Territory; 'Qld', Queensland; 'SA', South Australia; 'WA', Western Australia.

[continued]

Table 3.2 (cont.)

[1] The second fledgling was found dead on the presumed day of fledging (Schoenjahn 2011b).
[2] At the same location on 31 May 2011, two adults accompanied by two juvenile birds were recorded. This was almost certainly the same family. Note that two offspring were recorded in May but only one in September. The site was a nesting site in 2010 when two young fledged; in 2011, however, the site was not used by Grey Falcons for breeding.
[3] The juvenile bird(s) received food from a parent.
[4] This pair was breeding at the time with three young in the nest.
[5] At the same location in late May 2012, two adults accompanied by one juvenile bird were recorded. This was presumably the same family as observed on 7 Oct. 2012 but with one of the two juveniles not having been detected the previous May.
[6] At the same location in mid-March 2012, two adults accompanied by two juveniles were recorded, almost certainly the same family. Although two offspring were recorded in March 2012, only one was seen on 17 Oct. 2012. The site was not a nesting site in 2012 nor in 2011, but in 2010 it was.
[7] This group was observed at that site until 2 Nov. 2009, i.e. beyond the cut-off date 31 Oct.

Table 3.3 Records involving juvenile Grey Falcons only, i.e. no adults observed, made between 15 Mar. and 31 Oct. 2007–2016 (n = 8). The records numbered 1–5 and 7 were made available to me by independent observers (names indicated) and were supported by photographic evidence, which allowed me to ascertain the age of the birds. Note that in all eight cases adults were not searched for and may have been overlooked.

	Month	Day	Year	State	Number of juveniles	Observer
1	Apr.	18	2010	NSW	1	T. Mutton
2	May	13	2013	Qld	1	S. Vernon and S. Knights
3	June	9	2015	NT	1	R. Waring
4	July	18	2012	SA	2 [1]	R. Clemens
5	July	7	2016	NT	1	P. Barratt
6	Aug.	6	2008	WA	1	J. Schoenjahn
7	Aug.	26	2014	WA	1 [2]	A. Boyle
8	Oct.	19	2009	Qld	2 [3]	J. Schoenjahn

[1] Three weeks earlier, i.e. on 29 June 2012, two juveniles were photographed by P. Waanders at a location 236 km to the NE. The birds involved may have been the same individuals because Grey Falcons at that age are capable of flying such distances within the given period (Chapter 4). The observation was, therefore, excluded from the analysis.
[2] The photos show that this juvenile was in very poor conditions: it was emaciated, had an empty crop, on both wings some primaries were missing and some others broken, and some rectrices were broken. All this must have handicapped the bird severely. The location was near Broome, north-western Australia, about 390 km NE of the nearest breeding location and outside the breeding distribution determined during this study.
[3] The two yearlings were observed briefly at a nest where two young had fledged in 2008, presumably involving the same individuals.

Table 3.4 Behaviour of Grey Falcons in family groups (n = 18), and assessment of the level of execution of selected skills of juveniles in these groups. Groups involved one or two adults ('ad.') and one or more of their presumed offspring from the previous year ('juv.'). Observations concern the periods from 15 Mar. to 31 Oct. (2007–2016), to cover juvenile ages 5–12 mo after fledging. 'n/a', not applicable, e.g. outside the breeding season; 'n/o', behaviour not observed; 'n / m', n out of m nights of observation, i.e. number of nights, n, during which at least one juvenile and one parent roosted together, against the number of nights, m, at which at least one member of the respective family was recorded roosting; 'b/a', below adult-standard execution of skills and manoeuvres. ' ' (blank), indicates that a behaviour or skill could not be assessed or a below adult-standard performance was not detected (see text).

	Month/year	Number and age (if known) of birds in the group	Site was breeding site in the prev. year	Adult behaviour			Family roosted together at night (n / m)	Juv. solicited	Motor skills in juv.			
				breeding	aggressive toward juv.	fed juv.			flying	selecting a suitable perch	precision landing	food handling /passing
1	03/2015	1 ad., 1 juv.	no	n/a	n/o	n/o	n/a	yes	b/a		fail	b/a [1]
2	04/2014	2 ad., 1 juv.	no	n/a	n/o	n/o	n/a	yes				
3	04/2008	2 ad., 2 juv.	yes	n/a	n/o	n/o	4 / 4	yes	b/a	fail	fail	
4	05/2008	2 ad., 1 juv.	yes	n/a	n/o	n/o	4 / 4	yes		fail	clumsy	
5	05/2016	2 ad., 2 juv.	yes	n/a	[2]	[2]	[2]	[2]	[2]	[2]	[2]	[2]
6	08–10/2007	2 ad., 1 juv.	not known	no	yes [3]	n/o	9 / 9	yes				
7	08/2008	1 ad., 1 juv.	not known	no	n/o	n/o	1 / 1	yes				
8	08–09/2011	2 ad., 1 juv.	yes	no	n/o	n/o	1 / 2	yes	b/a			
9	09/2009	1 ad., 1 juv.	yes	no	n/o	n/o	1 / 4	n/o	b/a	fail [4]		
10	09/2008	1 ad., 1 juv.	not known	no	n/o	n/o	1 / 1	n/o				
11	09–10/2015	2 ad., 1 juv.	not known	no	n/o	yes [5]	4 / 4	yes	b/a			see [5]
12	09–10/2015	2 ad., 1 juv.	not known	yes [6]	n/o	yes [5]	3 / 3	yes	b/a		fail [7]	see [5]
13	10/2012	2 ad., 1 juv.	yes	no	n/o	n/o	1 / 1	yes			clumsy	clumsy [8]
14	10/2012	2 ad., 2 juv.	no	no	n/o	n/o	1 / 1	n/o				
15	10/2012	3 (≥1 ad., ≥1 juv.)	not known	no	n/o	n/o	1 / 1	yes				
16	10/2012	1 ad., 1 juv.	yes	no	n/o	n/o	1 / 1	yes				
17	10/2009	2 ad., 1 juv.	yes	no	n/o	n/o	1 / 1	yes				
18	10/2016	2 ad., 2 juv.	yes	no	n/o	yes [5]	3 / 3	yes	clumsy		clumsy	clumsy [9]
	Total		≥9 in 18	1 in 13	1 in 17	3 in 17	36 / 40	14 in 17	juv. below ad.-standard in 9 of 17 families			

[continued]

Table 3.4 (cont.)

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[1] The juvenile fed on a small passerine bird when I arrived at the site. It took the juvenile 20 min to consume the item which may have been an Australasian Pipit *Anthus novaeseelandiae* (body mass 26 g (Higgins et al. 2006)). By contrast, adults were repeatedly observed in this study taking about one minute to consume a Budgerigar *Melopsittacus undulatus* (body mass 30 g (Higgins 1999)).
[2] This family was observed for a few minutes only, roosting together in the morning before flying off unnoticed. Behaviours and skills could not be assessed and are therefore omitted from the totals.
[3] See text for details.
[4] The juvenile abandoned multiple approaches to land near the perched adult female and finally flew away.
[5] A juvenile received food from a parent, i.e. either the parent fed the juvenile piecemeal or a whole prey item was passed from adult to juvenile. In all cases both birds were perched and the prey was dead.
[6] This pair was breeding at the time with three young in the nest. Whether Grey Falcons bred in this area in the preceding year, 2014, is not known. Refer also to Table 3.2, footnote [4].
[7] The situation concerned the site of an active nest (containing three nestlings at that time) of an adult pair, about 80 m above ground on a repeater tower. The 1-yr-old juvenile was perched on the structure near the nest when the adult male parent arrived with prey and perched at the level of the juvenile but on the opposite side. For more than three minutes the juvenile tried clumsily to find a way to walk, climb and hop along the structure to the adult male before it succeeded and took the food off its parent. The juvenile did not attempt to reach the parent by flying, as an adult bird would likely have done.
[8] The yearling fed clumsily on a food item, repeatedly taking it into the bill and making a few steps back or forth, then passing it back to one foot and pulled at it again, often failing to tear off meat. Holding it in one foot, the yearling looked at the item and tilted its head from one side to the other, a behaviour that I have not observed in feeding adults.
[9] One of these two yearlings, while soaring with a whole dead bird (that it had received from its male parent) in its talons, pulled with its bill on the item, dropped the item twice, each time catching the falling item in mid-air.

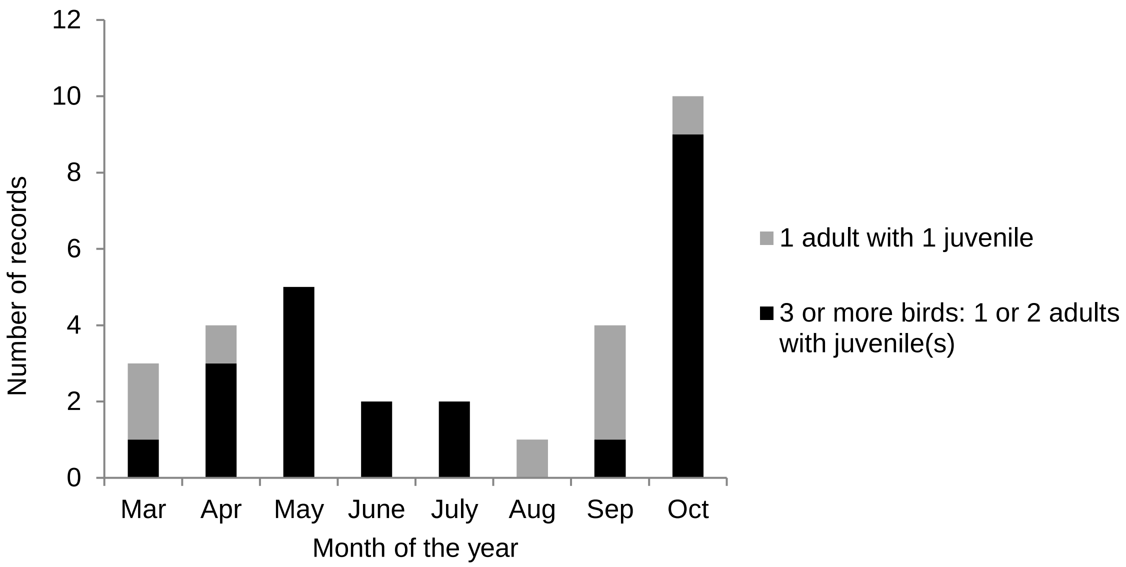

Figure 3.1 Frequency of records of Grey Falcon family groups observed between 15 Mar. and 31 Oct. 2007–2016 (n = 31).

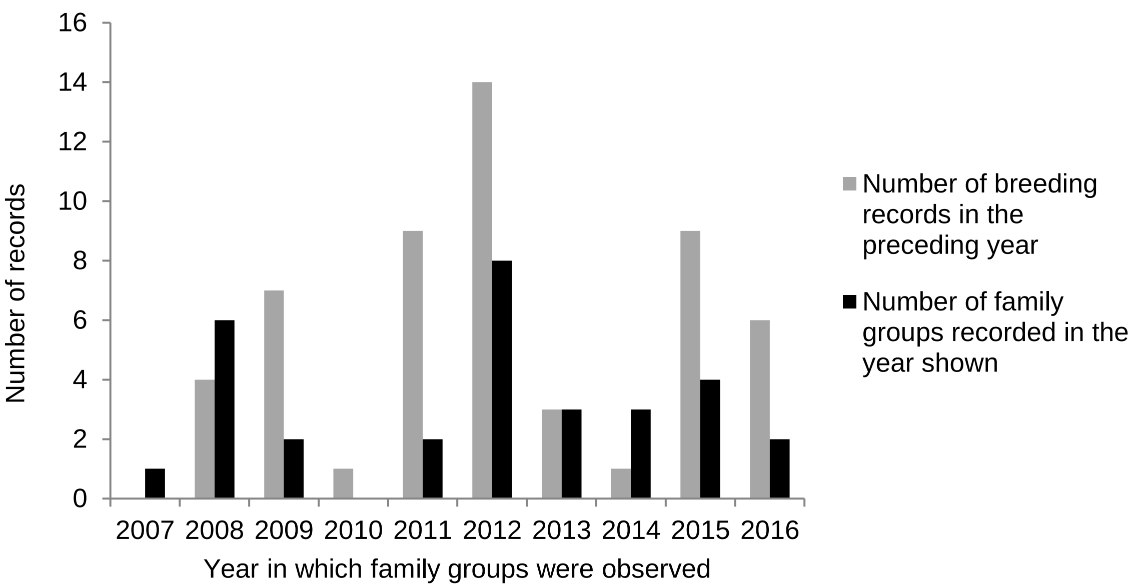

Figure 3.2 Frequency of records of Grey Falcon family groups observed between 15 Mar. and 31 Oct. of each of the years 2007 to 2016 (n = 31), and the number of breeding records for the preceding year (n = 54), i.e. the year in which the juvenile birds in any given year group hatched. Note that breeding was not recorded in 2006, but had evidently taken place. Same data as for Figure 3.1 but arranged by year.

Behaviours of parents and juvenile offspring

The behaviours of adult and juvenile Grey Falcons observed in individual family groups are presented in Table 3.4. Juveniles of all families that were assessed for night-roosting (100%; n = 15) roosted together with their parent(s) during most nights surveyed (89%; n = 38) 5–12 mo after fledging, i.e. during March–October. This behaviour was independent of the age of the juveniles. Of note, a family roosted together at night even after the male parent had attacked its single offspring from the previous season; the begging yearling was attacked several times on 6 and 7 Oct. 2007. This was the only instance in this study of a parent attacking a closely associated offspring. The family group was clearly attached to a nest in good repair but the adults did not breed in that year.

Begging or harassing a parent for food was observed in juveniles in most family groups (81%; n = 16), and this was seen frequently in these birds. The behaviour was independent of the age of the juveniles and was seen in individuals (n = 15) even 12 mo after fledging, i.e. between late September and late October. Juveniles in seven of eight families that were observed during these periods showed this behaviour (Numbers 11–18 in Table 3.4).

Parents providing food to their offspring 5–12 mo after fledging was recorded in three family groups (18%; n = 17) (Table 3.4). All these instances (n = 13) involved an adult pair associated with one or two offspring at the age of about 11–12 mo after fledging, and these were begging and harassing their parents, strongly at times. During four (31%) of these 13 instances, the adult parent fed the offspring piecemeal. In the remaining nine instances (69%), the offspring seized a whole prey item, or a part of it, from the parent's talons while both birds were perched (see below). The first pair involved in such feeding (No. 11 in Table 3.4) was not breeding at the time but was clearly attached to a nest in good repair which might have been the yearling's natal nest. The second pair (No. 12 in Table 3.4) was breeding at the time and had three nestlings. On 15 Sep 2015 the yearling was fed piecemeal by the adult female while both birds stood on the active nest. Later that day the yearling received a whole dead bird from the adult male. The third pair (No. 18 in Table 3.4) was closely associated with two yearlings; on 1 Oct. 2016 feeding of one or the other offspring was observed seven times. The location was a nesting site of 2015 where a pair had raised two young and almost certainly involved the same individuals.

During all 13 instances when a yearling received food from an adult, both birds were perched and the prey was already dead. Occasionally the yearling would fly a short distance to meet the food-delivering adult in the air and molest the adult, sometimes even trying to get hold of the prey. Invariably the adult would not let go of the prey but evaded the juvenile until all birds were perched. For example, a perched adult female did not let her 1-yr-old female offspring have the whole prey despite the yearling attacking the item; the adult then commenced feeding the yearling piecemeal.

Birds 5–12 mo after fledging were observed six times to feed on food that was not observed being received from an adult parent. These cases involved the family groups numbered 1, 11, 12, 13 (n = 2) and 18 in Table 3.4. In one of these cases (No. 12 in Table 3.4), the yearling was perched outside the nest when I arrived at the site and was feeding on a large grey bird, presumably a Crested Pigeon *Ocyphaps lophotes*. The latter species is one of the heaviest regular prey species of the Grey Falcon (Schoenjahn 2013). An hour later the yearling jumped onto the nest with about half of the prey item still in its foot. On the nest the brooding adult female took the item and commenced feeding the yearling, the three nestlings, and herself. Feeding by these birds and other juveniles may also have occurred out of view and is presumably under-recorded.

Birds younger than 12 mo after fledging were never observed catching their own prey. The yearling of family group No. 6 in Table 3.4 was observed at three separate instances taking a fast dive toward the ground and subsequently landing on the ground without having captured a prey item. It remains unclear whether these dives were aimed at a prey item because I failed to make out any such item in all these cases. Of the family group No. 3 in Table 3.4, I observed briefly one of the juveniles flying behind an adult that appeared to be hunting below treetop-level along a creek-line. Neither of the birds made a capture while within my view.

Motor skills of juveniles

Juvenile Grey Falcons (5–12 mo after fledging) in nine (53%) of the 17 families assessed had at least one key motor skill not fully developed, i.e. performed below adult standard (Table 3.4). The results were independent of the age of the juveniles. Specifically, young birds from 5 to 12 mo after fledging performed below adult-standard in three crucial skills, namely flying, landing on a selected spot, and food handling.

A further incidence of a young bird with below adult-standard motor skills involved an adult breeding pair and a yearling male, and these birds were not closely associated as a family group. None of these birds was marked and it remains unclear whether they were indeed parents and offspring (see below). Therefore, the incidence was not included in

Table 3.4. On 23 Sep. 2009, the yearling flew toward the pair's active nest (on a repeater tower) while both adults were present. The yearling begged incessantly and flew with inefficient wing-beats, lost height, and barely avoided collision with one of the cable guys of the repeater tower. The yearling was instantly driven away vigorously by both adults. The site might have been the yearling's natal nest site and the yearling might have been the offspring of one or both of these adults because a pair had nested at that site in 2008, raising a single male young.

Juvenile motor skills of below adult-standard were presumably under-recorded. This is because some tasks were not observed being performed or their performance did not require great skill. For example, food-handling skills could not be assessed in the cases when the juveniles were fed piecemeal, and flying in a locality as shown in Figure 2.1 may not often require difficult manoeuvres.

3.4 Discussion

The data show that it is typical for young Grey Falcons and their parents to stay together in a close family group for up to 12 mo after fledging. The high incidence of records involving juveniles 12 mo after fledging (Figure 3.1) suggests strongly that family members stay together even longer. Even at this advanced age of the young, the adults almost invariably showed no signs of aggression toward them (with the exception of one bird) and fed them. Key skills of these 1-yr-old birds were clearly well below the standard that typified the behaviour of adult birds, and this included their flying and food handling abilities. Importantly, they were occasionally fed piecemeal by their parents, i.e. in the same way in which nestlings and newly-fledged young are fed (Schoenjahn, pers. obs.). This feeding occurred even in those cases in which the parents were breeding in that subsequent season. I expand these points below in the light of the species' specializations with respect to diet and climate, and compare the behaviours of Grey Falcons with those of other raptors including other species of *Falco*.

Dietary and climatic specializations

The Grey Falcon's specializations in diet and climate, two fundamental ecological aspects by which the Grey Falcon stands out among all its congeners, were explored in Chapter 2. There I showed that the Grey Falcon's diet is the most restricted of any species in the genus *Falco*, consisting virtually exclusively of birds throughout the year and independent of age, and that it is the only species of *Falco* that is entirely restricted to a zone of arid climate with some of the highest average annual temperatures globally. I propose that the dietary and climatic specializations of the Grey Falcon influence the development of juveniles and result in the severely extended juvenile dependence that I have described here. This hypothesis is outlined below, and is followed by suggestions for testing it further.

Difficult foraging and reduced learning opportunities

The difficulty in learning to become nutritionally independent is the most common explanation in cases of slow juvenile development in a species (Ashmole and Tovar 1968, Burger 1980, Heinsohn 1991, Hunt et al. 2012). Most often invoked is the long time taken to learn intricate foraging skills that take a lot of repeated practice to learn. Examples of this situation are the fabrication and use of specific tools to excavate food from crevices by New Caledonian Crows *Corvus moneduloides* (Hunt et al. 2012) and extracting seeds by podomandibulation from the large woody nuts of Marri *Corymbia calophylla* trees by Forest Red-tailed Black Cockatoos *Calyptorhynchus banksii naso* (Johnstone et al. 2013). Also invoked for explaining cases of slow juvenile development is the difficulty in locating scarce food, for example in frigatebirds that scan the surfaces of tropical oceans for food, and then learn to snatch it from the ocean surface or from another bird (Nelson 1967, Burger 1980). The periods during which the fledged young of these and other species are supported by their parents with food are provided in Table 3.5.

Table 3.5 Examples of bird species with prolonged post-fledging periods during which adults support their offspring with food. See text for details of each case.

Species	Duration (months)	Explanation	Sources
Grey Falcon	12 or more	see text	this study
New Caledonian Crow	up to 10	Use of specifically fabricated tools to extract food from crevices	Hunt et al. (2012)
Great Frigatebird *Fregata minor*	≥ 6 *	‘The specialized ... feeding technique of snatching food in flight and piracy ... take a long time to perfect’	Nelson (1967, p. 318)
Forest Red-tailed Black Cockatoo	≥ 6	Handling of difficult food	Johnstone et al. (2013)

* Schreiber and Ashmole (1970) assumed that young Great Frigatebirds on Christmas Island were even fed for as long as 14 mo or more after fledging.

Young Grey Falcons face at least three difficulties. First, their almost exclusive prey items, live birds, are always difficult to pursue. Second, the species' dietary specialization evidently does not allow them to switch to prey types that may be easier to obtain at a given time. Third, the extreme climatic events that occur throughout the species' distribution may limit the young falcons' physical performance. I expand these points in the remainder of this section.

Bird prey is generally perceived to be the most difficult prey type to pursue, and learning to hunt birds effectively requires many attempts and, therefore, considerable time (Newton 1979). Because Grey Falcons feed virtually exclusively on birds, which they typically capture in the air (Schoenjahn, pers. obs.), juvenile Grey Falcons have to learn at the onset to hunt this difficult prey without being able to build up their skills gradually on flying prey that is less difficult to pursue, for example locusts and grasshoppers (see below). This gradual, staged learning is known from species of *Falco* and other raptors that are less specialized on bird prey than Grey Falcon. For example, Schuyl et al. (1936) reported that the young of three broods of Eurasian Hobby *Falco subbuteo* initially hunted only slow insects (Geotrupidae beetles), then included faster and more agile insects (dragonflies), but did not take birds (as adult Eurasian Hobbies do) during the observation periods ending 2, 3, and 5 wk after fledging, respectively. In the Peregrine Falcon, a bird specialist (Cade 1960, Ratcliffe 1980) that routinely includes significant proportions of other prey in its diet (Chapter 2), the young may pursue flying insects within a week of fledging (Cade 1982, Sherrod 1983). Snyder and Wiley (1976) reported that young Red-shouldered Hawks *Buteo lineatus* at 2–3 wk after fledging began to take insects and small amphibians as prey, but did not take larger vertebrates (including mammals) until 5–8 wk after fledging.

The Grey Falcon's extreme dietary specialization evidently stops them from switching to easier food sources or opportunistically taking available alternative prey when bird prey becomes more difficult to obtain. For example, a pair of Grey Falcons was observed flying through and perching amidst substantial swarms of Australian Plague Locust (*Chortoicetes terminifera*) without feeding on these insects (Schoenjahn, pers. obs., 24 Aug. 2010, Queensland). By contrast, the Black Falcon *F. subniger*, Australia's largest falcon and partly sympatric with the Grey Falcon, often feeds on locusts (Marchant and Higgins 1993, Debus and Tsang 2011, Charley et al. 2014, Debus et al. 2017). Also bird specialists like the Peregrine Falcon and Taita Falcon *F. fasciinucha*, readily make the switch to alternative prey (Chapter 2).

Grey Falcons of all ages show dietary specialization, but the normal environment of the species results in this dietary specialization being particularly challenging for the young. Specifically, the nestlings fledge at the beginning of summer, the season when extreme climatic events occur most frequently (e.g., extreme temperatures, persistent rain, and tropical cyclones) or are most severe (e.g., droughts, strong hot winds). During such periods live birds may be particularly difficult for inexperienced young Grey Falcons to find, let alone catch. In part, this difficulty results from the reduced activities of small birds in response to extremely hot conditions, when they seek shade more often and fly less than at other times, thus becoming more difficult to obtain for Grey Falcons. Also, prey abundance may be reduced during droughts or tropical cyclones, through migration and mortality. Even a few successive missed opportunities by an inexperienced bird could have fatal results (Ashmole and Tovar 1968, p. 94).

During summer, the pursuit of agile bird prey is likely to be physiologically more demanding than at other times because of the demands of the falcons' thermoregulatory requirements, especially when high humidity is coupled with high temperatures. Further, rain in the Grey Falcon's breeding area is most likely in summer (Schoenjahn 2013, particularly Figure 1) and will reduce foraging opportunities because wet plumage dramatically reduces their flight performance (Schoenjahn, pers. obs.). To illustrate this point, the foraging time of Yellow-eyed Junco *Junco phaeonotus* is limited during summer storms, to the extent that inexperienced (but independent) juveniles perished at significantly higher rates than dependent young (Sullivan 1988). A further factor may be the presumed lower resilience of the young Grey Falcons compared to adults, including their ability to endure periods of low food supply, especially when temperatures are very high. Indeed, their bird prey may be their only source of fluid, even during the hottest periods. In short, the young Grey Falcons' abilities to acquire food reliably and with dependable frequency are challenged, directly, by the climatic circumstances and the young birds' ability to endure periods of low food supply.

The considerations above may explain why young Grey Falcons require more time, perhaps much more, than the young of all other *Falco* species, especially since they fledge with the adverse circumstances that occur during summer in the arid zone of Australia. Even 6 mo after the end of summer, the 1-yr-old Grey Falcons still rely on their parents for food, and their flight and other survival skills are not fully developed (Table 3.4). By contrast, the young of all similar-sized raptors require no more than 3 mo from fledging to become nutritionally and otherwise independent. To explain this extraordinary discrepancy, the year-round behaviour of adult Grey Falcons needs to be considered.

Grey Falcon behaviour relative to Peregrine Falcon

Adult Grey Falcons have low activity levels throughout the year with respect to key behaviours (Chapter 2). These levels were shown to be much lower than in the Peregrine Falcon, with this interspecific difference being consistent through the year (Table 2.6). The latter species was chosen because Peregrines also typically hunt birds, although not as exclusively as do Grey Falcons, and the distribution of the Peregrine Falcon in Australia overlaps that of the Grey Falcon. Further, the Peregrine Falcon belongs to the group of eight species that include the closest relative of *F. hypoleucos* (Chapter 1).

Of particular significance is that Grey Falcon parents do not entice their young to practice skills that appear crucial for hunting and hence are crucial to their independent survival. For example, aerial adult-juvenile food transfers were not observed, i.e. neither talon-to-talon transfers nor the release of dead or live prey. Aerial food transfers are regarded as serving the learning of a crucial part of the predatory sequence that young raptors have to acquire to become nutritionally independent (Sherrod 1983). Indeed, the behaviour of releasing dead and live prey has been documented for Peregrine Falcons (for references see Table 3.6), Eurasian Hobbies (Tinbergen 1958), other raptors (e.g., Red-tailed Hawk *Buteo jamaicensis* (Bent 1937) and Hen Harrier *Circus cynaeus* (Beske 1978)), and also for a variety of other avian and mammalian predators such as terns, felids, and otters (as reviewed by Sherrod (1983)). Reduced learning incentives and practice opportunities were considered to hamper the development of fundamental motor skills in other bird species, for example in White-winged Choughs *Corcorax melanorhamphos* (Heinsohn 1991), and also in humans (Valentini and Rudisill 2004).

Evidently, the activity levels of adult Grey Falcons are low throughout the year with respect to key behaviours, and Grey Falcon parents even appear to keep activity levels of their young low, for example, by transferring food only when perched (Table 3.6). Elevated activity levels increase metabolic rates and hence endogenous heat production. For a warm-blooded animal living in an extreme and unpredictable environment, with solar radiation intense and ambient temperatures often well above body temperature, it is crucial that endogenous heat production is minimal. This is particularly true for birds, because heat dissipation in birds generally is limited, and largely restricted to respiratory evaporation (Schmidt-Nielsen 1964). I propose that the ecological answer of the Grey

Falcon to these challenges is behavioural; individuals maintain low activity levels throughout the year (Chapter 2). This is reflected also in that Grey Falcon parents keep the activity levels of their young low, even though this results in slow skill development. This, in turn, delays the independence of the young.

Table 3.6 Qualitative comparison of behaviours of Grey Falcon parents toward their offspring with those of Peregrine Falcons. The references relate to the latter species. 'Ad.', adult; 'juv(s).', juvenile(s) from the age of fledging to 1 yr.

Behaviour	Parent Grey Falcons	Parent Peregrine Falcons	Reference
Period during which fledglings are fed	Up to 12 mo, perhaps longer	≤ 3 mo	Newton (1979)
Piecemeal feeding of fledglings	Up to 12 mo, perhaps longer	May cease 2 wk after fledging	Sherrod (1983)
Ad.-juv. food transfer	Only when perched	Include aerial transfers from 2 wk after fledging	Treleaven (1977), Sherrod (1983)
Food item transferred	Food item dead in all cases	Include live prey released in the air, from 2 wk after fledging	Sherrod (1983)
Enticing juvs. to aerial food transfer	Not observed even 12 mo after fledging	During the first 3 mo after fledging	Sherrod (1983)
Enticing juvs. to follow them hunting	Not observed even 12 mo after fledging	From 3 wk after fledging	Sherrod (1983)

Implications for the parent Grey Falcons

Prolonged parental support should increase, in general, the survival chances of the offspring (Burger 1980, Ekman and Griesser 2002). If, however, the prolonged support of offspring from a given season interferes with the parents' breeding activity in the subsequent season, the survival chances of the offspring from both seasons may be reduced (*sensu lato* Trivers 1974). In this section I argue that Grey Falcons, by contrast, may increase their reproductive success by supporting their previous year's young into the next breeding season.

Grey Falcon pairs can breed in consecutive years (see above), in line with all other members of the genus *Falco* (Cade 1982), but may, quite regularly, not do so (Table 3.7). If they do not breed in a given year, other pairs of Grey Falcons in the same general area may also not breed in that year (see below). The behaviour of a pair may therefore be largely independent of the specific circumstances of the pair (e.g., loss of a partner) and the individuality of the partners, but may be governed by other, more general, circumstances. These are most likely environmental conditions. This interpretation is supported by the spatiotemporal distribution of recorded breeding events for western, central, and eastern parts of Australia (Table 3.7). Further, the presence of five family groups in October 2012 in Queensland where breeding was not reported for that year but where six pairs had been found breeding in the previous year suggests that the environmental conditions there in 2012 were sufficient for these family groups to survive, but not suitable for Grey Falcons to breed.

Table 3.7 Frequency of breeding records 2007–2016 (n = 57) for the states and territories of Australia, arranged from west to east. Breeding was not recorded during this period for the two south-eastern states of mainland Australia, namely New South Wales and Victoria.

Year	Western Australia	Northern Territory and South Australia	Queensland
2007	1	1	2
2008	0*	1	6
2009	0	0*	1
2010	0	2	7
2011	3	5	6
2012	3	0*	0*
2013	1	0*	0*
2014	1	2	6
2015	2	3	1
2016	0	3	0*

* During the breeding season of the year indicated, non-breeding adult Grey Falcons, single or paired, were found at one or more former breeding sites (since 2007) of the species and/or in the general area of such a site.

This pattern of reproduction suggests that the environmental conditions within any given part of the Grey Falcons' breeding distribution may become temporarily unsuitable for breeding, and that this may occur quite commonly. Therefore, by not breeding in a given year, pairs should not necessarily be seen as simply missing a breeding opportunity. Foregoing breeding may rather be a response of the adults to less than ideal conditions. Indeed, breeding for Grey Falcon was not recorded during this study in areas that were affected by severe and/or prolonged droughts (Chapter 1).

The following picture emerges. The decision of a pair to breed or forego breeding in a given year is influenced by environmental conditions. Regardless of whether a pair breeds, they may continue supporting their (surviving) offspring from the previous year. In the rare instances that a pair breeds while still associated with their offspring from the previous year, they provide food to both broods. In each case the adults do not miss a breeding opportunity, and, therefore, potentially enhance their lifetime reproductive output by offering prolonged support to their offspring.

Further research

The duration of time during which family members stay together is currently not clear. Likewise, it is not known what process triggers the eventual breakup of families. Many juveniles remain with, and appear to depend on, their parents for 12 mo or longer after fledging. Of the 39 independent records of one or more Grey Falcons that involved at least one juvenile at the age of 5–12 mo after fledging (Tables 3.2 and 3.3), 31 (79%) involved also at least one parent, in seven cases (18%) adults were not searched for and may have been present but overlooked, and in only one case (3%) (No. 7 in Table 3.3) it seemed that the juvenile, about 10 mo after fledging, was not closely associated by a parent (its apparent emaciation and damaged remiges suggest that this juvenile likely was no longer supported and protected by a parent). The juvenile-parent association in Grey Falcons was shown to persist even when the parents bred again in the following year. Particular environmental conditions may play a role in the termination of the extended juvenile-parents association in the Grey Falcon because the species' extreme environment appears to exert a strong influence on other key behaviours (hunting, movements, agonistic behaviour). Also, the individuality of each family member involved may come into play. Further investigations that involve the simultaneous satellite-tracking of adults and young from the same family, are needed to provide clarification on these behaviours. Long-term studies covering multiple breeding seasons and a variety of environmental conditions, and involving family groups from across the species' distribution, seem most desirable.

3.5 Conclusion

The extended juvenile dependence in Grey Falcons is without parallel among species in the genus *Falco* and other raptors of similar size. The extraordinary behaviour of members of a family of Grey Falcons to stay close together as a group into the next breeding season may be explained by the following postulates.

First, the Grey Falcon is the only member of the genus *Falco* that is specialized absolutely, i.e. at all ages and throughout the year, to take only bird prey, one of the most difficult types of food to obtain. Learning to capture birds and not being able to build up skills by hunting easier prey, such as insects, is difficult and takes many attempts. It thus requires many learning opportunities, which results in a comparatively prolonged learning period.

Second, Grey Falcons breed exclusively in the arid and semi-arid zone of Australia, and the first season that the newly-fledged young have to endure is summer. The extreme and unpredictable climatic events that characterize these environments reduce the learning opportunities for the young, and thus further prolong the learning process for the young.

Third, the Grey Falcon is the only member of the genus *Falco* that is restricted absolutely to environments of the hottest climate zones of the world. The Grey Falcon is adapted behaviourally to these hot environments by maintaining low activity levels throughout the year, and this is reflected in the way that the parents bring up their young. The behaviours of the parents toward their young seem to require the interpretation that they entice their young to keep activity levels low. Low activity levels of the young, however, result in slow skill development, which in turn prolongs the dependence of the young.

Table 3.8 Published incubation and nestling periods of the species of *Falco* found in Australia. Data taken from the summaries compiled by Marchant and Higgins (1993), unless stated otherwise.

Falco species		Mean weight male, female (g)	Incubation period (d)	Nestling period (d)
F. subniger	Black Falcon	630, 900 (582 [1], 833 [1])	estimated 34, ~34 [2]	38–49, 42–42 [3]
F. peregrinus macropus	Peregrine Falcon	600, 890	averaged 33 [4]	39 [4], 38–42
F. berigora	Brown Falcon	470, 625	31–34	36–41
F. hypoleucos	Grey Falcon	412 [5], 502 [5]	~35 [6]	~38 [7], 49–52 [6]
F. longipennis	Australian Hobby	210, 290	28–35	32–41
F. cenchroides	Nankeen Kestrel	165, 185	28–29	26–35

[1] Average weight of free-flying individuals (males, n = 11; females, n = 18) (Debus and Olsen 2010).
[2] Debus et al. (2017) (n = 1).
[3] Charley et al. (2014) (n = 1).
[4] Average of 20 nests, with nestling periods ‘varying considerably between nests’ (Pruett-Jones et al. 1981, p. 257); range not provided.
[5] Median weight of free-flying individuals, this study. See Chapter 2.
[6] Cupper and Cupper (1980) (n = 1). See Chapter 1.
[7] Ley and Tynan (2016) (n = 1).

Fourth, the extended period of juvenile dependence appears to be related to slow learning rather than to slow embryo and chick growth rates because incubation and nestling periods in Grey Falcons are within expectations for their size when compared to the other Australian falcons (Table 3.8).

In conclusion, the slow skill development and the consequential extended dependence of the young Grey Falcons may be seen, ultimately, as adaptations to the species' environment, Australia's arid and semi-arid zone, one of the hottest environments in the world.

Chapter 4

Movement ecology of the Grey Falcon in arid Australia – a reluctant nomad in an extreme environment

4.1 Introduction

Movement is a fundamental feature of an organism's ecology (Andrewartha and Birch 1954). It allows individuals to probe their environmental surroundings, and thus find areas that, at that time, have the potential to maximize their chances of survival and reproduction (Walter and Hengeveld 2014). Questions as to why and when animals move, where they go, and what triggers these movements continue to intrigue (Dingle 1996, Nathan et al. 2008). In particular, the movements of highly mobile birds, capable of flying extreme distances, have attracted much research attention, and this includes birds of prey (Falconiformes) (e.g., Bildstein and Zalles 2005, Bloom et al. 2011, Burnham and Newton 2011, Braham et al. 2015).

For birds, five major patterns of movements have been distinguished: resident or sedentary, dispersive, migratory (i.e. conducting seasonal to-and-fro trips), irruptive, and nomadic (e.g., Roshier and Reid 2003). Classification of a particular species into any one of these categories is, however, not straightforward. This results partly from the difficulties in drawing the line between these categories (Baker 1978, Dingle 1996) and the resulting inconsistency with which most of these terms have been used. Further, a given species may fit into more than one category. For example, members of a species may be migratory in one part of the species' distribution but sedentary in other parts (White at al. 1994).

Dean (2004, p. 1) identified two basic movement patterns used by desert birds to cope with the harsh conditions of their extreme environment: (1) to be resident and sedentary, which implies that the individual must use its behavioural and physiological adaptations to withstand, *in situ*, the desert climate and unforeseeable extreme weather events and fluctuations in food availability, and (2) to move opportunistically or seasonally to areas where conditions are suitable and resources available.

Among the 38 species that make up the genus *Falco* (del Hoyo and Collar 2014), 30 species are considered to be sedentary to some extent. In only seven species may the movements be interpreted as nomadic (Appendix 2). The movements of the two endemic Australian falcons that are most strongly associated with the arid zone, the Grey Falcon and Black Falcon *F. subniger*, are considered to be poorly understood and these birds are thought to be nomadic to some extent (White et al. 1994). Published observations on short-term (i.e. daily) movements of Grey Falcons are unavailable. Their long-term (i.e. seasonal) movements have, however, generated a range of (contradictory) opinions in the literature. These perspectives encompass the spectrum of movement patterns from resident or sedentary to partially migratory to highly irruptive. These perceptions were presented, and critically assessed, in Chapter 1.

A proper understanding of the movements of the Grey Falcon, a highly mobile raptor that persists in the extreme environment of the Australian arid zone, is key in understanding its ecology. Specifically, movements may constitute a crucial means for these birds to evade unfavourable conditions and persist in a hot environment characterized by episodes of boom and bust that are unpredictable in regard to occurrence, severity, and duration. To gain an insight into their day-to-day and long-term movements I satellite-tracked seven individuals and supplemented that data by on-ground observations that included individually colour-banded birds. This is the first study conducted on movements of marked Grey Falcons.

My objective was to determine the short- and long-term movement patterns of Grey Falcons and how these are influenced by climatic conditions. Specifically I sought to establish whether the day-to-day movements of these animals are influenced by local climatic conditions, for example high daytime temperatures, and test whether the species can be characterized by the novel term 'reluctant nomad', which would be defined by the following pattern of movements. (i) After breeding, birds stay in the area and breed in consecutive years as long as conditions are suitable. (ii) If conditions in the subsequent season are not good enough to breed but good enough to survive, then they stay – better conditions may be too far away and difficult to find – but do not breed. (iii) If conditions present a risk even to survival, then they move on – it must be better somewhere else.

This definition delimits a reluctant nomad from a 'typical' nomad and a resident species in the following way. A resident remains in the area of its residency during its entire life. Food caching, aestivation and torpor are examples of the behavioural and physiological means that enable the individual to cope with the desert environment *in situ*, and thus remain resident. A ‘typical’ nomad does not possess behavioural or physiological adaptations to remain sedentary once conditions deteriorate. The nomad follows favourable environmental conditions across regions, its movements are unpredictable, unseasonal and irregular, and it may not return to an area previously occupied for months or years (Dean 2004). Furthermore, most nomads breed opportunistically in space and time (Dean 2004). By contrast, a reluctant nomad remains in an area for as long as conditions support survival, and even foregoes breeding if environmental conditions are not good enough for breeding, but good enough for survival. Only once the conditions present a risk even to survival, for example during extreme food shortage or weather, will the reluctant nomad move to a new area.

4.2 Methods

Movement data from wild Grey Falcons were collected between July 2003 and June 2017. The general fieldwork methods and study area have been described by Schoenjahn (2013). Twenty free-flying wild birds, including one that got released after two weeks in rehabilitation, were colour-banded using methods described by Schoenjahn (2011b). Nestlings were not captured because of the risks inherent to the procedures. Of the 20 birds banded, nine were selected to be fitted with solar-powered Doppler-shift platform transmitter terminals (PTTs, hereafter called transmitters) (Table 4.1). Birds selected were at least 6 mo old and assessed to be healthy and fit. Birds younger than 6 mo were excluded from satellite-tagging because it appeared early in the study that Grey Falcon juveniles develop flying and other crucial survival skills later than expected for a species of *Falco* (Chapter 3). Seven Grey Falcons (four females, three males) were satellite-tracked for periods between 82 d and 797 d (median 119 d) between September 2009 and October 2015 (Table 4.1). The total tracking time was 2001 bird-days. The tracking data of two further satellite-tagged birds, No. 8 and 9 in Table 4.1, were excluded from further analysis because the behaviour of both birds may have been affected by adverse circumstances; see Table 4.1 for details. Additional movement data were obtained from on-ground observations, which included observations of colour-banded individuals. Further, after breeding was recorded at a location, that location was revisited during most subsequent breeding seasons to establish whether Grey Falcons bred there again or were present. Visiting every breeding site, once known, during each subsequent breeding season was impeded by logistical constraints.

Table 4.1 Details of the nine birds that were satellite-tracked. Dates are given as dd/mm/yy. PTT 141276 was used on a second bird after being retrieved and refurbished, and therefore appears twice, as bird Argos ID 141276 (Qld) and bird Argos ID 141276 (NT).

	Argos ID	Sex	Age	Area	Body mass of bird (g)	Relative mass of PTT	Deployed	Data end	Fate of bird	Data (days)
1	54142	♀	adult	Barkly Tableland, NT	486	3.3%	19/09/09	15/01/10	Not known, PTT ‘died’ [1]	119
2	79109	♂	adult	Barkly Tableland, NT	339	3.5%	09/10/10	13/04/12	Not known, PTT stationary [2]	553
3	134881	♀	7 mo	W. Pilbara, WA	447	2.1%	04/04/14	08/06/16	Eaten by a Wedge-tailed Eagle [3]	797
4	141276	♂	adult	SE Qld	396	2.4%	07/10/14	27/12/14	Eaten by a feral cat [4]	82
5	141628	♀	adult	W. Qld	498	1.9%	13/10/14	07/01/15	Alive, seen after it shed PTT [5]	87
6	141276	♂	adult	W. Simpson Desert, NT	412	2.3%	30/09/15	01/01/16	Died, reason not known	94
7	150861	♀	adult	NE SA	582	1.6%	11/10/15	05/07/16	Not known, signal lost	269
8	150860	♀	adult	N. Pilbara, WA	555	1.7%	24/05/16	04/06/16	Dead, human interference? [6]	12
9	162913	♀	adult	W. Simpson Desert, NT	476	2.0%	06/10/16	10/10/16	Alive, seen after it shed PTT [7]	5

[1] The time that elapsed between ON-periods increased slowly and the signal was eventually lost. The bird appeared to have moved around normally during the time it was tracked.

[2] The signal became stationary but ceased before I reached the site to search for the PTT. A bush fire destroyed the unit a few days before my visit. Although the bird’s fate is not known, it is possible that the weak link of the harness failed and freed the bird, which would be within expectations because it was 18 mo that the harness and transmitter had been on the bird. The weak links used on the harnesses in this study are expected to break after about two years. The bird was seen last on 22 Sep. 2011 at the nest, which contained one young.

[3] The PTT and feather remains of the falcon were found beneath a regular feeding roost of a Wedge-tailed Eagle *Aquila audax*.

[4] Remains of the bird, including skull, wings, and many feathers, were found in a cave-like opening at the base of a small thorny bush, and scattered around the immediate area. I assumed that the falcon had fallen prey to a feral cat *Felis catus*. The ‘cave’ appeared much too small for a canine, including Dingo *Canis lupus dingo*, and, perhaps, also too small for a European Red Fox *Vulpes vulpes*; foxes are typically larger than feral cats, and are found only occasionally in the area concerned, a locality in the Barcoo Shire of Queensland (Biosecurity Queensland https://www.daf.qld.gov.au/__data/assets/pdf_file/0019/73810/IPA-Fox-PA13.pdf, accessed 31 May 2017), whereas feral cats are common in that area (Australian Government http://www.environment.gov.au/biodiversity/invasive-species/feral-animals-australia/feral-cats, accessed 31 May 2017).

[5] Two month after the signal was lost I saw the colour-banded bird, freed from transmitter and harness, at the breeding site of 2016, in company of an adult male.

[6] The bird was tagged when released from two weeks in rehabilitation; the dead bird and its intact PTT were found at a rubbish tip. Human interference may have been involved in the movements and the fate of that bird. Therefore, the satellite tracking data were excluded from further analysis.

[7] The bird did not accept the transmitter and continued, during the 24 hr that I monitored it after tagging, pulling on the harness. The transmitter with harness were found beneath the nest, the harness with a loop bitten off. Because the behaviour of this bird was affected by the transmitter, I excluded the satellite tracking data from further analysis. On 15 Apr. 2016, i.e. six months after having shed the transmitter, the colour-banded bird was seen and photographed by a volunteer.

The transmitters were attached to the birds as backpacks by means of individually fabricated harnesses, a standard method for attaching this type of transmitter to raptors, including falcons, of similar size to Grey Falcon (e.g., Peregrine Falcon *Falco peregrinus* (Fuller et al. 1998); Prairie Falcon *F. mexicanus* (Steenhof et al. 1999); Sooty Falcon *F. concolor* (Javed et al. 2012); Lesser Kestrel *F. naumanni* (Limiñana et al. (2012)). The harnesses were made of tubular Teflon® tape with a flattened width of 6.35 mm (1/4 inch), provided by Bally Ribbon Mills, Bally, PA, USA. The harness design included a weak link, which consisted of household cotton sewing thread that was used to stitch the upper and lower harness loops together. The weak link was designed to break when the cotton thread disintegrated after about two years, or if, for example, the bird got entangled in vegetation. The satellite-tracking was carried out by CLS/Argos, Toulouse, France (http://www.argos-system.org).

Accuracy of the satellite-generated location data

The satellite derived location estimates of Doppler-shift transmitters do have errors associated with them (CLS 2014) and researchers have investigated extensively the size of these errors and how they impact on animal tracking studies (e.g., Steenhof et al. 2005, Nicholls et al. 2007, Patterson et al. 2010, Douglas et al. 2012). Therefore, before attempting to analyse the location estimates in this study, I determined the magnitude of these errors. Two principally different models of transmitters were used in this study, differing in their duty-cycles. The North Star models used on the birds Argos ID 54142 and 79109 transmitted exclusively during daylight hours (Table 4.2), i.e. when the movement speed of the tagged bird was not known. The Microwave model that was used on the remaining birds transmitted a 10 hr ON – 24 hr OFF cycle and thus periodically during parts of the night, i.e. between sunset and sunrise, when the birds were stationary. That Grey Falcons remain stationary at night was established during this study by direct observation of individuals during and outside the breeding season. The difference between the two types of duty-cycles impacted on the interpretability of the location data as explained below.

The North Star units were tested (in Australia but outside the study area, and only when stationary) before deployment with the result that the accuracy of the data appeared adequate to determine the general area that a tagged bird uses, and insufficient for the reconstruction of their flight paths with any great accuracy. This stemmed partly from the

Table 4.2 Details of the eight solar-powered Doppler-shift transmitters used in this study. Repetition cycles were 60 seconds, and nominal output power 200 mW. CLS/Argos applied the Kalman filtering algorithm to all data. Note that the transmitter 141276 was used on two birds (see Table 4.1 for details).

Argos ID	Manufacturer	Model	Mass (g)	Transmission regime
54142	North Star [1]	16G Solar BirdBorne PTT	16	Dependent on direct solar energy, no energy stored
79109	North Star	12G Solar BirdBorne PTT	12	Dependent on direct solar energy, no energy stored
134881	Microwave [2]	9.5g Solar PTT-100	9.5	10 hr ON 24 hr OFF
141276	Microwave	9.5g Solar PTT-100	9.5	10 hr ON 24 hr OFF
141628	Microwave	9.5g Solar PTT-100	9.5	10 hr ON 24 hr OFF
150860	Microwave	9.5g Solar PTT-100	9.5	10 hr ON 24 hr OFF
150861	Microwave	9.5g Solar PTT-100	9.5	10 hr ON 24 hr OFF
162913	Microwave	9.5g Solar PTT-100	9.5	10 hr ON 24 hr OFF

[1] North Star Science and Technology, King George, VA, USA.
[2] Microwave Telemetry, Inc., Columbia, MD, USA.

circumstance that during daytime the birds cannot be assumed to be stationary and therefore location estimates cannot be gauged other than by comparison with the bulk of the estimates. However, the general area that a tagged bird used during a sedentary period (see results) could be determined, and also the time of the bird’s shift from one such area to the next.

The Microwave model was tested extensively on stationary transmitters in the study area (see below). Their accuracy was sufficient to determine, as with the North Star models, the general area used by a tagged bird. In addition, the data often allowed to approximate paths of wide-ranging flights. This was possible because a roosting tagged bird generated a cluster of location estimates if it was ‘seen’ by multiple satellites. These clusters allowed, in many cases, the bird’s night-roost location and, occasionally, day-roost location to be determined within 350 m (see below). The precision of the approximated roost locations aided the reconstruction of wide-ranging flight paths.

In summary, the accuracy of the location estimates corresponds with the accuracy that the testing of the research hypothesis requires (as recommended by Christin et al. (2015)).

The approximation of a night-roost site from a cluster of location estimates was achieved in a two-step process. First, the estimates from that night (sunset to sunrise) were plotted on satellite imagery of the earth's surface (freely available from GoogleEarth https://www.google.com/earth/). Obvious outliers could so be visualized and then eliminated. Only those nights for which at least three estimates were available were considered. After removal of the outliers, the means of the estimates' latitudes and longitudes were computed. The 'approximated location' was created by using these means as its latitude and longitude. Means were used rather than medians because they produced better results in the following performance test. I tested the performance of this two-stepped method on the data from the transmitter ID 141276 (Qld) after it had become stationary in the study area; its true location was obtained *in situ* with a handheld GPS device (GPS 315, Magellan Corp., San Dimas, CA, USA). Of 10 locations approximated in this way, all were within 350 m of the transmitter's true location, and eight of them within 200 m (Table 4.3). The elimination of the visually identified outliers improved the accuracy of the method substantially, reducing the median error from 390 m to 139 m.

All satellite-tracked birds in this study were captured at sites where they roosted regularly. The sites were either active nests or known or assumed nest sites of a previous year. Before being captured, the respective bird invariably night-roosted on the nest-tree or a nearby tree, or on the artificial structure that supported the nest. If an approximated night-roost location was within 500 m of the site where the bird was tagged, the tagging site was taken as the bird's location of that night.

On-ground observations

On-ground observations, including those of individually colour-banded birds, were included in the analyses. For breeding events, I computed the rainfall amount reported at the nearest weather station during the nine months (Oct.–June) that preceded the respective breeding season (the breeding season commences in July (Chapter 3)). That period was chosen because a 3-mo time lag for the aggregation of environmental data was shown by Runge et al. (2015) to be the best predictor for the occurrence of arid-zone nomadic species, and the period January to June appears relevant for the nomadic Grey Falcon when selecting an area for breeding. In addition, many of the Grey Falcon's prey species are nomadic to some extent or their population size fluctuates greatly in response to environmental conditions. These species include Budgerigar *Melopsittacus undulatus*, Diamond Dove *Geopelia cuneata*, and Zebra Finch *Taeniopygia guttata* (for lists of prey species see Marchant and Higgins (1993), Schoenjahn (2013); for details of these species see *Handbook of Australian, New Zealand and Antarctic Birds* (1990–2006)). Rainfall data were provided by the Australian Bureau of Meteorology (http://www.bom.gov.au), as were long-term temperature records. Maps that show the paths of tropical cyclones were provided by Australia Severe Weather (http://www.australiasevereweather.com/).

Table 4.3 Performance of the method to approximate a night roost location from the ARGOS location estimates for that night. Shown are the performance results for the first ten 10-hr ON-periods of transmitter ID 141276 (Qld) after it became stationary. ‘Error’, great-circle* distance from the known true location of the transmitter; ‘Location ($\overline{x}_{Lat}$/$\overline{x}_{Lon}$)’, a geographic location created by computing the means of the latitudes (i.e. $\overline{x}_{Lat}$) and longitudes ($\overline{x}_{Lon}$) of the estimates from this ON-cycle and using these means as the location’s geographical coordinates (the approximated locations were created in the same way but after removing the visually identified outliers, see text).

	Frequency of estimates	Range of the estimates’ errors (m)	Error of the location ($\overline{x}_{Lat}$/$\overline{x}_{Lon}$) (m)	Frequency of outliers	Error of the approximated location (m)
1	8	64–1057	196	1	144
2	8	224–1826	724	3	330
3	7	64–3913	168	2	133
4	9	64–4162	519	1	122
5	4	90–3456	807	1	107
6	6	124–1703	494	2	162
7	4	128–725	138	1	63
8	9	28–1114	127	1	60
9	9	136–2227	402	1	199
10	7	90–1852	378	1	345
1–10	71	28–4162	127–807 [1]		60–345 [2]

* Calculations are based on the assumption that the earth is a perfect sphere with the radius r_e = 6378.137 km, the earth’s equatorial radius (NASA Space Science Data Coordinated Archive https://nssdc.gsfc.nasa.gov/, accessed 12 June 2017).

[1] Median = 390.

[2] Median = 139.

4.3 Results

The satellite-derived data from seven wild Grey Falcons from across the species distribution were analysed. The day-to-day movements of these individuals were, during periods ranging from six weeks to six months, confined to circles with radii of 20 km in most cases. The shift of an individual from one such quasi-sedentary area to the next was in each case preceded by one or more wide-ranging trips, ranging from about 20 km to more than 1000 km. During these trips the birds visited areas as distant as 330 km away from their respective regular day-to-day area at that time. The execution of these trips was independent of the maximum daytime temperature. The furthest shift between two consecutive areas of quasi-sedentary movements was 77 km. In regard to breeding, of the 40 nests monitored, six were used in two consecutive years, and a further nest was used in three consecutive years. In those cases in which birds bred in consecutive years, the rainfall for the breeding event in the second year was similar to or greater than that for the breeding event in the first year.

The geographic distribution of the areas that the satellite-tracked birds used is shown in Figure 4.1. The short- and long-term movement patterns of the satellite-tracked individuals (n = 7) are summarized in Table 4.4. The movements of bird Argos ID 134881 are illustrated in Figure 4.2, those of bird Argos ID 141276 (Qld) in Figure 4.3.

The day-to-day movements of all satellite-tracked birds were confined to circles with radii ranging from 10 to 30 km, and 20 km in most cases. During these periods the birds, unless breeding, night-roosted at many different locations throughout the respective circle (e.g., Figure 4.2C). I term this behaviour therefore as quasi-sedentary. When breeding, i.e. between egg laying and fledging of the young, the satellite-tracked parents spent most but not all nights at the nest and their day-to-day movements stayed within circles of 10–20 km radii. Four birds (Numbers 2, 3, 5, and 6 in Table 4.4) that were not breeding changed the respective areas of their day-to-day movements gradually or after having undertaken wide-ranging trips. The periods for which a bird’s quasi-sedentary movement patterns remained unchanged ranged from six weeks to six months. The furthest shift between two consecutive areas of quasi-sedentary movements involved bird Argos ID 134881 and was 77 km (Figure 4.2C).

The wide-ranging trips ranged from single-day trips to multi-day trips and from 18 km to 282 km distance between consecutive night-roosts, with the actual flight paths possibly being considerably longer. These trips occurred during quasi-sedentary periods (Figure 4.2A,B) or marked the transition from one such period to the next (Figure 4.2D,E).

The most expansive multi-day trip involved bird Argos ID 134881 which covered a distance greater than 994 km in nine days; the cumulated distance between night-roosts being 844 km (Figure 4.2B). During this trip the bird visited areas 330 km away from its regular day-to-day area at that time (Figure 4.2B). The wide-ranging movements of this individual during the passing of a tropical cyclone are summarized in Table 4.5.

The male Argos ID 141276 (Qld) night-roosted at the active nest during 18 out of 24 nights with known night-roost locations (covering the period from 7 Oct. to 15 Nov. 2014), and then roamed across an area of 12,861 km^2 until its death on 27 Dec. 2014 (Figure 4.3). During the latter period the bird spent only one night at the nest and covered distances of up to 124 km between two consecutive night-roosts.

The influence of local weather conditions on the birds’ movements showed in the following ways. The maximum daytime temperature was irrelevant for the occurrence of wide-ranging trips (Appendix 5). Such trips were undertaken during periods with temperatures repeatedly reaching as much as 45ºC. Localized rain appeared to have triggered a short-range shift of day-to-day activity by bird ID 134881. This was recorded in a chance observation. On 4 Apr. 2014, the then 7-mo-old bird was found with its parents 25 km from its natal site at a location where an unknown amount of rain had fallen locally about two weeks before my visit and had triggered considerable fresh plant growth. By contrast, the area around the nest was considerably drier at that time and without fresh plant-growth. A further climatic event that triggered a response of a Grey Falcon was a tropical cyclone (TC). In March 2015, the passing of TC Olwyn appeared to have triggered a spontaneous extensive movement of bird ID 134881 (Table 4.5). The behaviour of the then 1½-yr-old bird in the face of the cyclone may be interpreted as follows. On 12 Mar., the bird reacted to the increasing wind force by returning to its most often used roost site during that period, the tagging site, and, after experiencing considerable winds and the onset of rain during the night, it flew, on 13 Mar, away from the cyclone’s path in a perpendicular direction for at least 145 km, i.e. presumably far enough for the wind to be within a range that the bird experiences routinely, and for the rain to be much less.

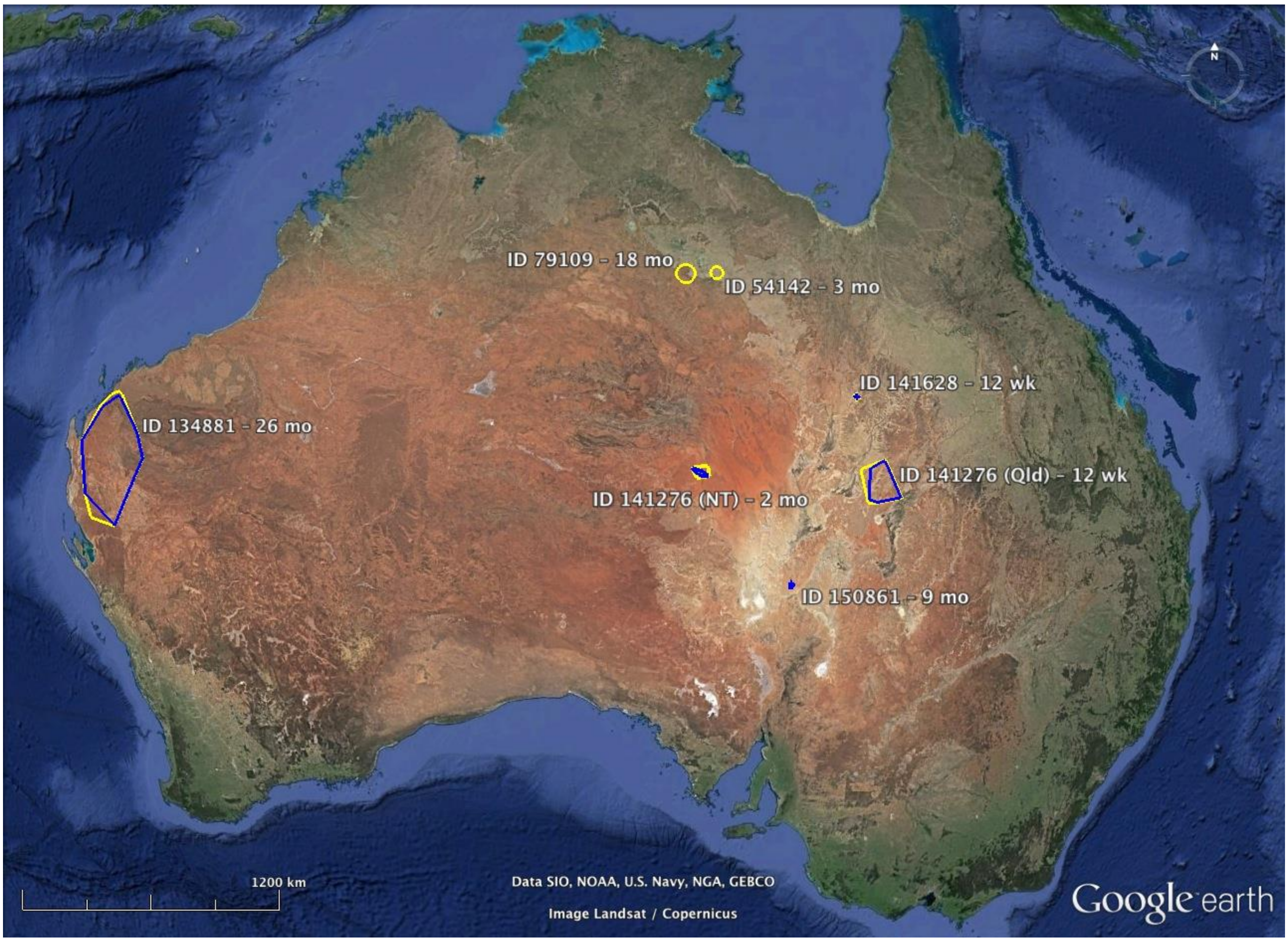

Figure 4.1 Geographical distribution and approximate sizes of the tracking areas of the satellite-tagged birds (n = 7) (Argos ID numbers and length of the tracking period indicated). The yellow circles encompass the respective movements of the birds No. 1 and No. 2 in Table 4.1; both birds had transmitters that transmitted during daytime only. The yellow convex polygons encompass the respective movements of the birds No. 3–7 in Table 4.1, the blue convex polygons encompass their night-roost locations; the transmitters of these five birds allowed the night-roost locations to be established (see text).

Figure 4.2 Movements of bird Argos ID 134881, Pilbara region of Western Australia. The bird was tagged on 4 Apr. 2014 at the age of about 7 mo, whilst it was still closely associated with its parents (see Chapter 3). It was satellite-tracked until its death on 8 June 2016. Night-roost locations (red pins labelled ‘N’) are shown with dates (dd/mm/yy). Day-roost sites are indicated likewise (red pins labelled ‘D’ and ‘day-roost’ added). The different maps illustrate movements of this bird at specific times within this period.
A) Wide-ranging trips (n = 8), illustrated by light-blue lines, during the period 3 Aug. to 16 Oct. 2014. All these trips were round-trips that started and ended at a night-roost location near the centre of the yellow circle. The yellow circle (r = 10 km) indicates the bird’s day-to-day movements for this period other than these eight round-trips. The one-way distances of the overnight roosts from the start/end-point are: 64 km, 3 Aug.; 27 km, 16 Aug.; 102 km, 21 Aug.; 136 km, 25 Aug.; 72 km, 1 and 19 Sep.; 68 km, 8. Sep.; 58 km, 10 Oct. Note that two trips involved the same overnight roost (1 and 19 Sep.).

[continued]

B)

Figure 4.2 (cont.)

B) Simplified flight path 22–29 Mar. 2015. The straight segments of the light-blue line connect the verified daytime location estimates and night-roost locations. The yellow circle (r = 20 km) indicates the day-to-day movements from 1 Dec. 2014 to 20 June 2015, excluding the wide-ranging trips pictured and two such trips that are not illustrated (on 21 Apr. and 29 Apr., involving one-way distances of 83 km and 21 km, respectively). Start and end-point of the wide-ranging trips pictured was the tagging site, located about 25 km from the bird's natal site. The length of the light-blue line is 994 km, the actual flight path was, conceivably, considerably longer. The greatest straight distance between the start point and a night-roost location was 288 km (night of 24 Mar. 2015).

[continued]

C)

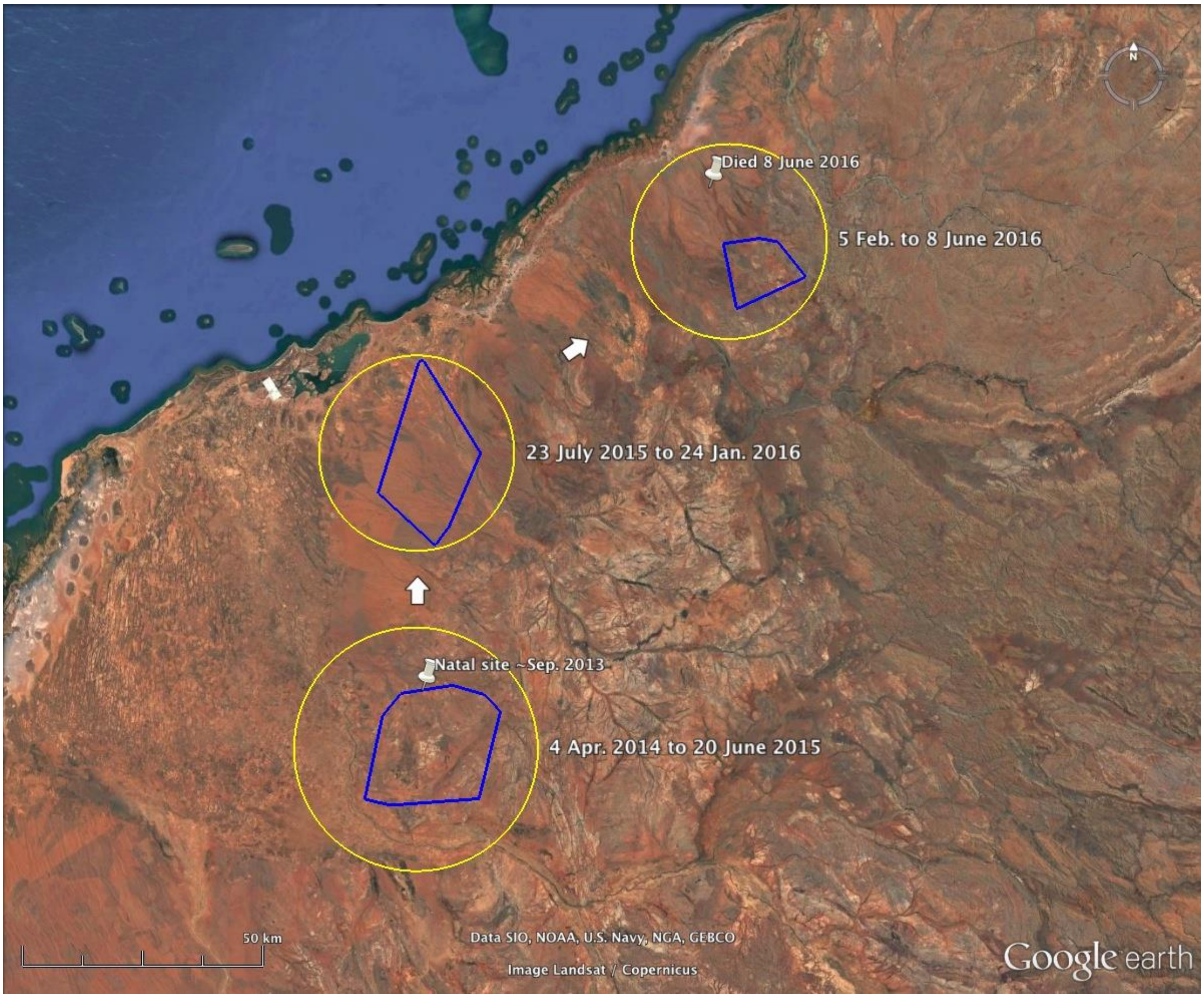

Figure 4.2 (cont.)

C) The bird's shifting of the area of its day-to-day movement over time. The yellow circles encompass the respective areas during the periods indicated. The radii are 25 km (4 Apr. 2014 to 20 June 2015), 20 km (23 July 2015 to 24 Jan. 2016), and 20 km (5 Feb. to 8 June 2016). The blue convex polygons encompass the night roost locations during each respective period. The area sizes are 526 km^2, 426 km^2, and 149 km^2, respectively. The distances between the middle points of the yellow circles, from south to north, are 60 and 77 km, respectively.

[continued]

D)

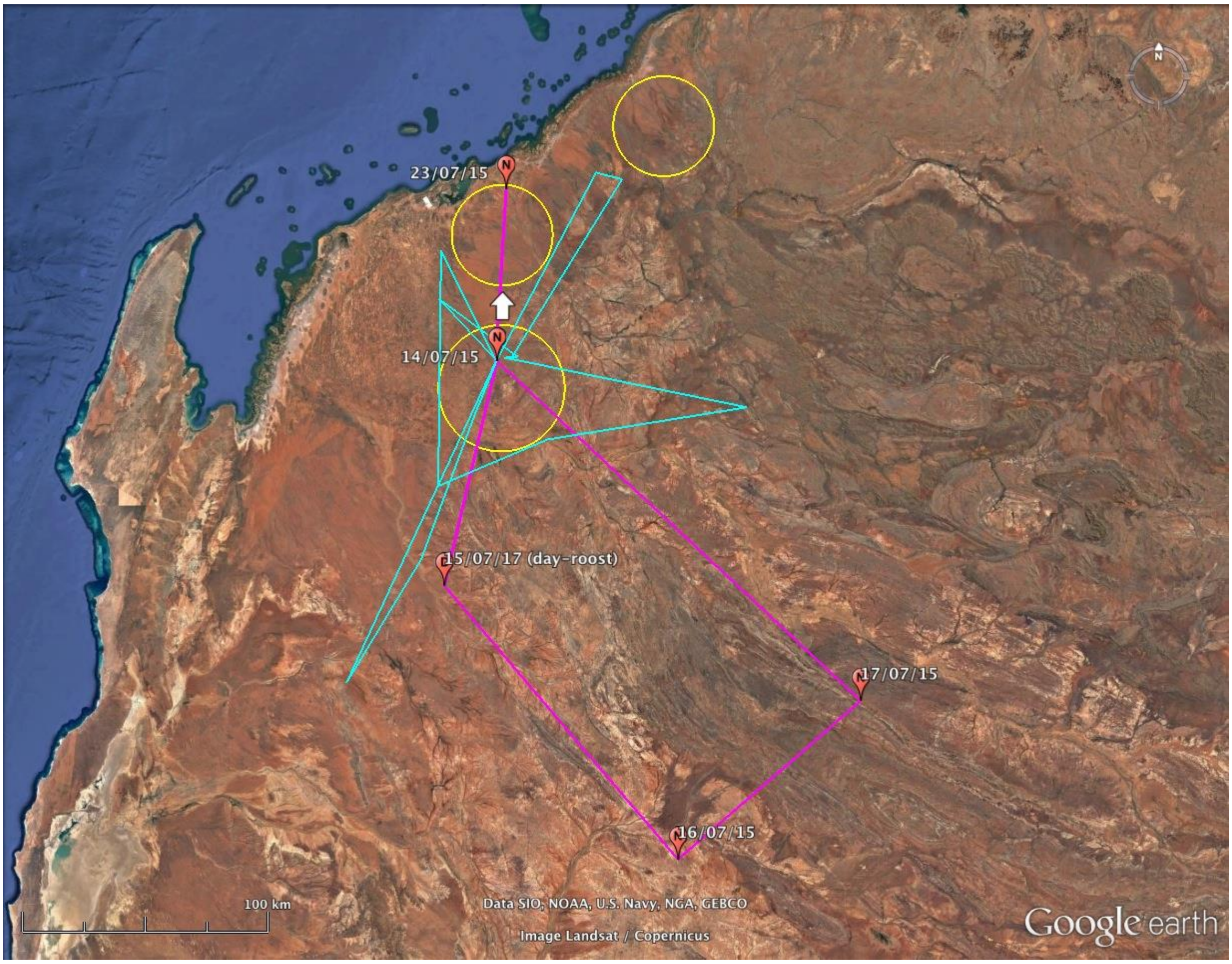

Figure 4.2 (cont.)

D) The wide-ranging trips that preceded the bird's shift from the first, southernmost day-to-day area to the second such area, 60 km to the north. The light-blue line connects the night-roost locations of the period 22 June to 9 July 2015, a total distance of 901 km. The purple line connects the night-roost locations and a day-roost site of the period 14–23 July 2015, a distance of 594 km. The latter trip brought about the aforementioned shift. The yellow circles were explained in Figure 4.2C.

[continued]

E)

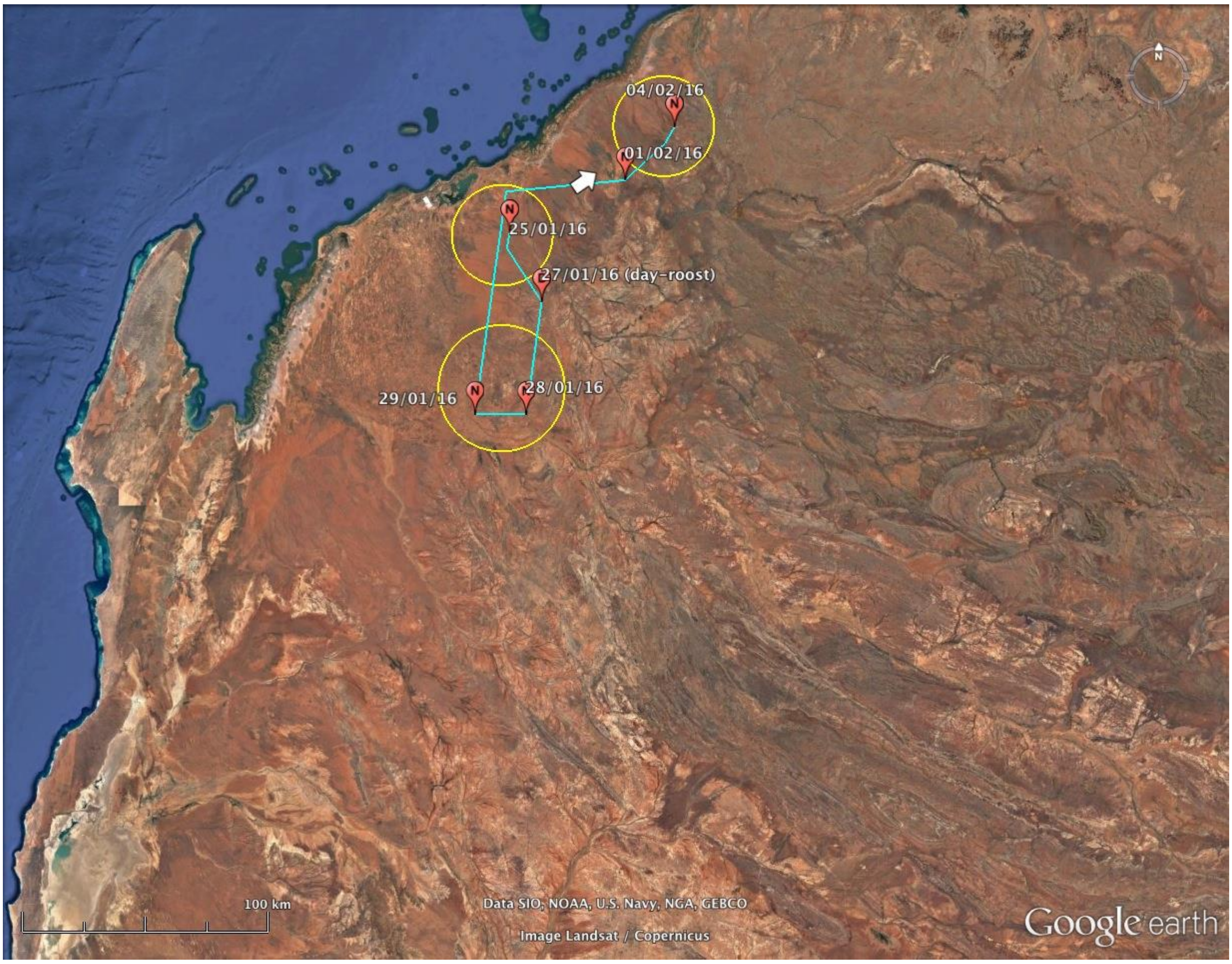

Figure 4.2 (cont.)

E) The wide-ranging trip that brought about the bird's shift from the second day-to-day area to the third, northernmost such area, 77 km to the north-east. Same image detail of the earth's surface as Figure 4.2D. The light blue line connects the night-roost locations and a day-roost site of the period 25 Jan. to 4 Feb. 2016, a total distance of 261 km. The yellow circles were explained in Figure 4.2C.

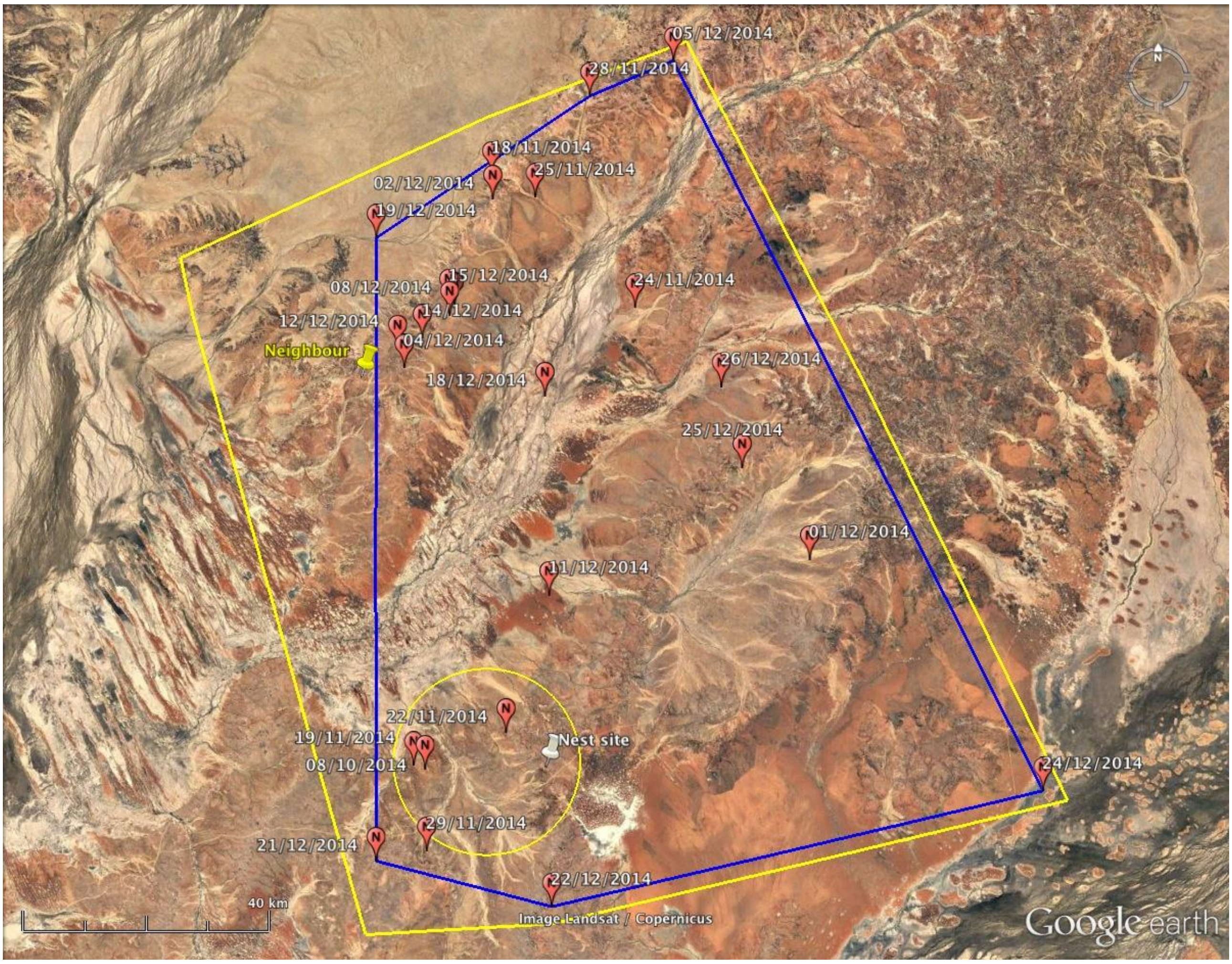

Figure 4.3 Movement patterns of bird Argos ID 141276 (Qld), tagged on 7 Oct. 2014 while breeding (nest location indicated). The yellow circle (r = 15 km) encompasses the bird's day-to-day movements during 7 Oct. to 15 Nov. 2014. The yellow line indicates the area (12,861 km^2) of the bird's movements during the period 17 Nov. 2014 to its death on 26 Dec. 2014, and the blue line indicates the area (9,622 km^2) covered by night roosts. During the former period, in 18 out of 24 nights with known locations the bird roosted at the nest site. During the latter period, in 25 nights with known locations (red pins labelled 'N'), the bird used the nest site only once (night of 9 Dec. 2014, not pictured). The dates shown refer to the date of the respective night. Straight distances between consecutive nights during the latter period range from 7 to 124 km (28–29 Nov.) Also shown, near the NW corner of the yellow polygon, is the location of the nearest known active nest of a neighbouring breeding pair of Grey Falcons. The distance between the two active nests is 69 km.

Table 4.4 Summary of the movement patterns of the satellite-tracked Grey Falcons. See Table 4.1 for details of the tagged individuals. A circle encompasses the area that a bird used, according to the satellite derived location data, in its day-to-day movements during the period indicated. The end of a period is defined as the day from when on the bird moved regularly out of the circle. The circles of consecutive periods may overlap partly or fully or are disjunct. '–', the bird remained within the circle. 'N/A', this period was dominated by the bird's wide-ranging movements and a circle that encompasses the bird's few shorter movements during that period is, therefore, not provided; note that these periods are comparatively short.

	Argos ID	Sex	Age	Period (dd/mm/yy)	Radius (km) of circle for day-to-day movements	Circumstances and comments	Greatest distance (km) between two consecutive nights
1	54142 [1, 2]	♀	adult	19/09/09–15/01/10	20 [1]	When tagged, the bird was associated with a 1-yr-old male.	[1, 2]
2	79109 [1, 2]	♂	adult	09/10/10–03/02/11	20 [1]	The bird was breeding when tagged.	[1, 2]
				04/02/11–29/05/11	15 [1]	Activities gradually shifted to an area about 18 km east of the nest (the bird bred in this nest in 2010 and 2011).	[1, 2]
				30/05/11–11/07/11	15 [1]	Activities shifted gradually back toward the nest.	[1, 2]
				12/07/11–20/11/11	20 [1]	Breeding at same nest as in the previous season. Another Grey Falcon pair is breeding 40 km away.	[1, 2]
				21/11/11–05/02/12	identical circle as previous [1, 3]	While remaining within the same circle, the bird's activities contracted somewhat and shifted gradually away from the nest, and then shifted back to the nest. [3]	[1, 2]
				06/02/12–13/04/12	20 [1]	The centre of the circle is near the nest. Signal became stationary on 13 Apr. 2012.	[1, 2]
3	134881	♀	7–11 mo	04/04/14–02/08/14	15	When tagged, the bird was closely associated with its parents.	–
			~1 yr	03/08/14–13/10/14	10	Wide-ranging single- and multi-day trips (e.g., Figure 4.2A). Many nights in an area of 0.4 km^2 but, evidently, not breeding.	136
				14/10/14–01/03/15	<20	Many nights in an area of 1 km^2.	(≥ 142 [4])
			~1.5 yr	02/03/15–29/03/15	N/A	Various wide-ranging trips (e.g., Figure 4.2B).	282
				30/03/15–18/06/16	20	Two over-night trips, 21 and 29 Apr. 2015.	82
				22/06/15–23/07/15	N/A	Various wide-ranging trips. The final trip, 594 km cumulated distance between 10 night-roosts, ended at the next quasi-sedentary area.	140
			~2 yr	23/07/15–24/01/16	20	During 21 Aug.–31 Oct., 33 of 49 known night-roosts were within an area of 0.4 km^2 (Figure 4.2B). Not breeding.	–
				25/01/16–04/02/16	N/A	10-day trip of a total of 261 km between the 11 night-roosts. The trip ended at the final quasi-sedentary area.	47
			29–33 mo	05/02/16–08/06/16	20	The bird was seen last on 9 May 2016 at a potential nest site in company of an adult male.	31

[continued]

Table 4.4 (cont.)

	Argos ID	Sex	Age	Period (dd/mm/yy)	Radius (km) of circle for day-to-day movements	Circumstances and comments	Greatest distance (km) between two consecutive nights
4	141276 (Qld)	♂	adult	07/10/14–15/11/14	15	Breeding; 18 of 24 known night-roost locations at nest. Another Grey Falcon pair is breeding 69 km away (Figure 4.3).	–
				18/11/14–26/12/14	N/A	24 of 25 known night-roost locations were away from the nest (Figure 4.3). Two 6-d and two 7-d trips with average distances between consecutive night-roost sites ranging from 47 km to 53 km.	124
5	141628	♀	adult	13/10/14–07/01/15	10	Breeding, subsequently associated closely with mate and an offspring. 42 of 49 known night-roost locations were at the nest, the remaining seven locations were within 12 km of the nest.	–
6	141276 (NT)	♂	adult	30/09/15–24/11/15	15	Non-breeding, associated with female partner and a 1-yr-old offspring. 35 of 37 known night-roost locations were at the nest.	–
				26/11/15–01/01/16	30	The bird expanded its day-to-day movements to an area within a circle of r = 30 km, covering about 1610 km^2. Five of 23 known night-roost locations were outside the circle of the previous period, eight were at the nest. The bird died at a location 30 km from the nest.	33
7	150861	♀	adult	11/10/15–06/04/16	20	Breeding when tagged, no further field observations. 100 of 101 known night-roost locations were at the nest, one night (20 Nov. 2016) was spent 6 km away from the nest.	–
				07/04/16–05/07/16	identical circle as for previous period	Eight of 51 known night-roost locations were away from the nest; the greatest distance from the nest, and also between two consecutive nights, was 18 km.	18

[1] The bird undertook no multi-day trips outside its regular day-to-day area at that time, notwithstanding that the bird may have occasionally left the area for some hours or even a night.

[2] The accuracy of the satellite derived location estimates was unsuitable for the identification of night-roost sites and reconstruction of flight paths (see text).

[3] Although the bird's movements during this period contracted somewhat and shifted slightly within the previous circle, they were best described by the previous circle.

[4] Day trip ≥142 km in total, reaching as far north as the next quasi-sedentary area. Before and after that trip the bird night-roosted at the tagging site.

Table 4.5 Details of severe Tropical Cyclone (TC) Olwyn and the movements of bird Argos ID 134881 during the cyclone's passing in March 2015, Pilbara region of Western Australia. The bird was positioned east of the cyclone's path at all times. The summarized cyclone data were provided by Australia Severe Weather (http://www.australiasevereweather.com) based on data from the Australian Bureau of Meteorology (http://www.bom.gov.au). 'Wind speed', estimated 10-min average wind speed near the centre of the cyclone.

Date of 2015 (dd/mm)	Time (hr)	Wind speed (m/s)	Central air pressure (hPa)	Approximate distance between the bird and the TC's centre (km)	Activity of bird Argos ID 134881
11/03	1800	26	990	570	Settled for the night.
12/03	0600	31	980	325	Started flying north against an increasing wind, thereby decreasing the distance to the intensifying cyclone.
	1800	39	955	160	Settled for the night 37 km north of the previous night, with the cyclone at its closest and strongest [1].
13/03	0600	36	970	335	Started flying east, i.e. in a perpendicular direction away from the path of the weakening cyclone.
	1800	21	990	580	The bird flew at least 145 km in 12 hours.

[1] The average wind speed at the location of the bird is estimated to have been less than half of the wind speed at the centre of the cyclone.

Rainfall amounts for areas in which breeding was recorded are shown in Table 4.6. Breeding (n = 59) occurred in areas where between 50 and 1133 mm of rain had fallen in the nine months before the start of the breeding season. The frequency of the breeding events in relation to the total amount of rainfall, and summarized from Table 4.6, is shown in Figure 4.4. The median rainfall for those areas and times in which Grey Falcons bred was 396 mm. Six of the 40 individual nests were used in two consecutive years, a further nest was used in two consecutive years, and, after a gap of two years, was used yet again for two consecutive years. One nest was used in three consecutive years. Of the nests that were used in two consecutive years, one nest involved the same pair, and one nest involved at least the same male partner (Table 4.6, footnotes 2 and 3, respectively). The identities of the individuals involved in the other consecutive breeding events are not known.

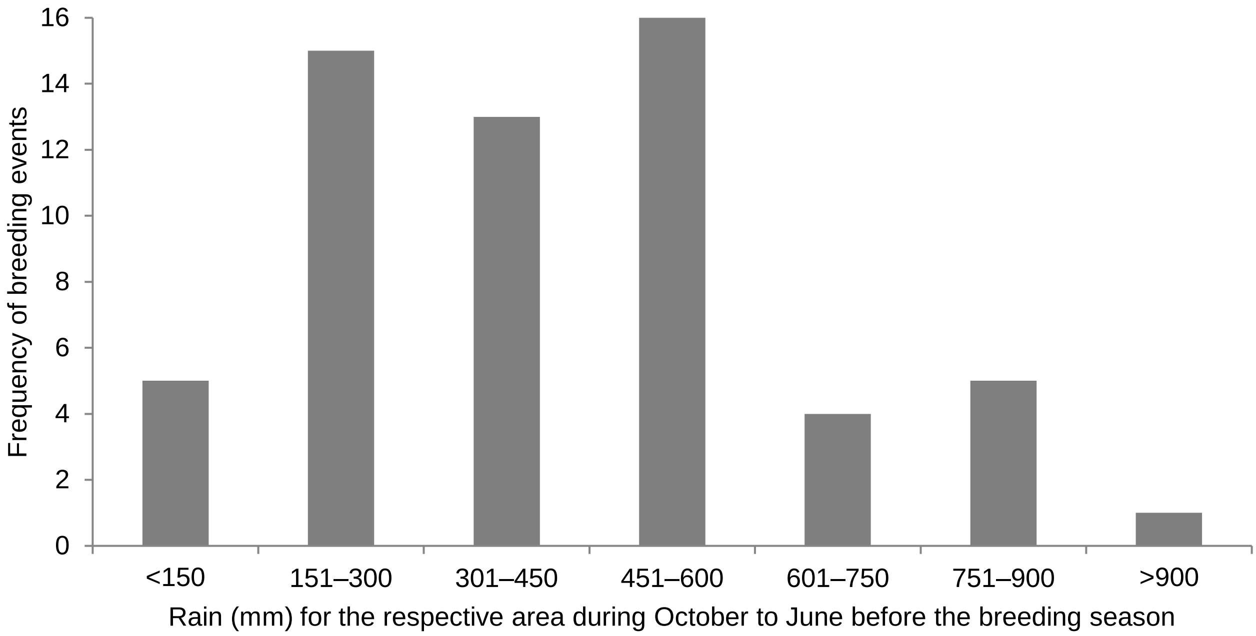

Figure 4.4 Frequency of recorded breeding events (n = 59) in relation to precipitation during the nine months October to June before the respective breeding season. Period 2003–2016. Same data as for Table 4.6 but arranged by ranges of rainfall amount.

The sites of 52 of the 56 breeding events of 2003–2015 (see Table 4.6) were revisited during the respective immediate subsequent breeding season. In 11 (21%) of the 52 cases Grey Falcons were encountered but were not breeding. These cases include family groups involving one or two adults and one or more yearlings, see Chapter 3. In 30 cases (58%) no Grey Falcons were encountered. In 11 cases (21%) Grey Falcons bred at the same location, invariably using the same respective nest as in the preceding breeding season. In addition to these 52 sites, Grey Falcons were recorded at a further five sites during the breeding season of one year (but not breeding then), and then found breeding in the year immediately after. In most of the cases mentioned in this paragraph the individuals were presumed to be the same individuals as were recorded at the respective location the year before (see Chapter 3 for further details).

Table 4.6 Areas for which breeding was reported, and the rainfall amounts (mm) for the nine months (Oct.–June) before the breeding season of the year indicated. ‘Area’, name of the weather station (http://www.bom.gov.au/climate/data/); ‘N’, total number of nest sites known for this area during 2003–2016; ‘n’, breeding frequency in this area in the year indicated; ‘Blank’, breeding was not reported in that area in that year (but may have occurred). Rainfall amounts rounded to the nearest mm. Highlights indicate that in that area breeding was reported in subsequent years. Breeding was not recorded for the years 2004–2006. Totals: nest sites, 40; breeding events, 59.

	Area	Total rainfall during October–June										
		2003	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
1	Birdsville, Qld (N = 2)		50 [1] n=1			424 [2] n=1	396 [2] n=1				173 n=1	
2	Boulia, Qld (N = 3)		346 n=1				373 n=1			97 n=1		
3	Camooweal, Qld (N = 2)						861 n=2			334 n=1		
4	Cunnamulla, Qld (N = 1)		245 n=1									
5	Jundah, Qld (N = 1)			297 n=1								
6	Longreach, Qld [3] (N = 5)	261 n=1		322 [3] n=4	430 [3] n=1	570 [3] n=2				137 n=1		
7	Thargomindah, Qld (N = 1)			218 n=1								
8	Windorah, Qld (N = 5)					526 n=4	709 n=3			203 n=3	193 n=1	
9	Marree, SA (N = 2)										156 n=2	
10	Moomba, SA (N = 1)					371 n=1						
11	Alice Springs, NT (N = 1)						503 n=1					
12	Allambi, NT (N = 1)											281 n=1
13	Daly Waters, NT (N = 1)						1133 n=1			882 n=1		
14	Tennant Creek, NT (N = 4)			132 n=1		639 [4] n=1	854 [4] n=2			464 n=1		496 n=2
15	Paraburdoo, WA (N = 1)							397 n=1				
16	Port Hedland, WA (N = 6)		497 n=1				520 n=3	474 n=1		279 n=1	177 n=1	
17	Red Hill, WA (N = 2)							193 n=1	471 n=1		383 n=1	
18	Tibooburra, NSW (N = 1)	126 n=1										

[continued]

Table 4.6 (cont.)

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[1] Rainfall indicated pertains to Clifton Hills, the weather station closest to the nest site. For the year when breeding was recorded again for this site, 2015, rainfall data from Clifton Hills are unavailable. The nearest weather station for which rainfall data are available for 2015 is Birdsville. For the 9 mo before the 2007 breeding season, i.e. 1 Oct. 2006–30 June 2007, the rainfall amount reported for Birdsville was 69 mm.
[2] A pair bred in this area in 2010 and again in 2011, using the same nest. Both adults were individually colour-banded and thus individually identified.
[3] One of the five nests in this area was the only nest in this study that was used in three consecutive years.
[4] The male Argos ID 79109 bred in this area in 2010 and again in 2011, using the same nest.

4.4 Discussion

My study of the movement ecology of the Grey Falcon has demonstrated that the species is generally nomadic, albeit with a distinct element of reluctance. The nomadic behaviour and the reluctance are apparent in both the breeding data and the satellite-derived data, as follows.

The satellite-tracking data show that the species is highly mobile and that individuals occupy specific areas for prolonged periods. Individuals also occasionally undertake wide-ranging trips of up to several hundred kilometres, but only when not breeding. Between bouts of wide-ranging trips the birds use, in their day-to-day movements and for periods of several weeks or months, areas that can be circumscribed by a circle with radius often around 20 km. During these periods they may night-roost at many different locations (unless they are breeding), and the birds' behaviour during these periods may therefore be termed quasi-sedentary. The shift from one such area to the next may be either gradual or occur at the end of a wide-ranging trip. The latter behaviour implies that these birds probe the environmental conditions of their wider surroundings and move to another area if they consider the conditions to be better there. The observed movements were clearly unpredictable, unseasonal and irregular and thus meet Dean's (2004) definition of a nomadic bird species.

The breeding data show that nest sites were used for a single breeding event in most cases, only occasionally in two consecutive years, and exceptionally in three. (That pairs breed no more than once per year was shown in Chapter 3, and Schoenjahn (2013) showed that the species has a distinct breeding season, in line with most species in the genus *Falco* (White at al. 1994).) In those cases in which birds bred in consecutive years, the rainfall for the breeding event in the second year was similar to or greater than that for the breeding event in the first year. These observations, although involving only presence data, may be interpreted in a similar way to the satellite derived movement data above.

That is, pairs stay in an area and breed during one or two (and rarely three) consecutive breeding seasons, and move on presumably if conditions are deteriorating. Once they have moved on they may not return for years. The recorded extent of their movements indicates that these birds have the capacity to relocate to distant areas if need be. Importantly, they are capable of moving when it becomes necessary, i.e. regardless of weather conditions at that very moment, and even during periods of extremely high temperatures.

The literature provides support for the perception that the Grey Falcon is generally nomadic. In the absence of specific studies of movements of Grey Falcon this support stems from four strong pieces of circumstantial evidence. They were presented in Chapter 1 and are summarized below.

(i) Morse (1922) conducted a 13-yr bird survey in the Moree district, north-western NSW, and recorded breeding of Grey Falcon only once.

(ii) Between 1995 and 2014, T. Aumann conducted a study in an area west of the Macdonnell Ranges of central Australia and recorded breeding Grey Falcons only in 1997 and 2011 (Aumann (2001b), T. Aumann, pers. comm. 11 June 2015).

(iii) For the period 1980–1999, Martin and Royal's (2001) compilation of Grey Falcon records for eastern New South Wales showed that the species was not recorded in that area in the years 1984–1992. The authors found that the year 1999 yielded the highest annual number of records for NSW (eight records), and concluded that 'it appears that the Grey Falcon may have regained some of its former breeding distribution in central western New South Wales since 1990' (Martin and Royal 2001, p. 133–134).

(iv) For the Strzelecki Creek region in north-eastern South Australia, Falkenberg (2011) reported breeding four times for the 10 seasons 1982–85 and 1995–2000 combined, one breeding event in each of the years 1982, 1984, 1996 and 1998. For the subsequent period 2003–2016, I am aware of only one breeding record for this area, in 2010, despite intensive searches by independent observers and myself, and despite this area being visited regularly by birdwatchers and especially so during parts of the breeding season. Of note, the period 2003–2009 coincided with persistent drought conditions for that area; the drought ended in November 2009 (Bureau of Meteorology rainfall maps).

The reluctance in the nomadic behaviour of Grey Falcons shows in the species' spatio-temporal breeding distribution. Grey Falcons were found to breed presumably when conditions are suitable, stay on after breeding and breed in the subsequent season(s) if the conditions remain suitable for breeding, or stay on but forego breeding presumably if conditions are unsuitable for breeding, and move on presumably if conditions are unsuitable for survival. The satellite-tracking data also reveal an element of reluctance in the movements of these birds. The data show that the distances between two subsequent quasi-sedentary areas used by an individual were limited. The greatest such shift was 77 km. A possible interpretation is that these birds move no farther than absolutely necessary – better conditions may be too far away and difficult to find. In summary, the data suggest that Grey Falcons leave an area only when absolutely necessary, move no farther than absolutely necessary, and rather forego breeding than taking the risk of searching far and long for more favourable conditions.

4.5 Conclusion

This chapter presents a long-term study of the movement ecology of the Grey Falcon in which I show that the species has a unique approach to interacting with its environment which I term 'reluctant nomadism' (see definition above). Specifically, I show that individuals or pairs of the species remain in an area for some weeks or months, or even as long as two and rarely three consecutive breeding seasons, and then shift to a new area. The new and likewise temporary area may include parts of the previous area or it may be disjunct and distant to the latter. That is, the species' behaviour is generally nomadic, as has been suggested by the data from the few available long-term bird surveys. Importantly, however, this study shows, further, that these birds remain in an area even if conditions become inadequate for breeding, and rather forego breeding than move on. This suggests that they move on only when environmental conditions become unsuitable for their survival, i.e. when absolutely necessary. From satellite data it appears that when these birds move on they move no farther than absolutely necessary. The nomadic behaviour of these birds has, therefore, a distinct element of reluctance.

These insights into the species' ecology will provide a basis for future studies. The latter are warranted to elucidate the criteria by which these birds decide to breed, to stay and not breed, and to move on. An understanding of the movement ecology of the Grey Falcon is crucial when attempting to recommend conservation measures, which are desirable given the species' extreme scarcity over such a broad area. The findings of this research have also clear implications for assessing the conservation status of the Grey Falcon, and in particular for estimating population size and population trends. The conservation and management of the Grey Falcon is covered in the following chapter.

Chapter 5

Conservation of the vulnerable Grey Falcon – long-term study reveals unexpected threats

5.1 Introduction

Australia has experienced one of the greatest relative losses of native fauna of any country in the world (Loehle and Eschenbach 2012, Australia's Threatened Species Strategy, available from https://www.environment.gov.au). The major causes of extinction are, as on all other continents, anthropogenic habitat alteration (including degradation and loss), and the various impacts of invasive alien species (including introduced carnivores) (DEWHA 2009, Hoffmann et al. 2010). Further, Australia has one of the highest proportions of endemic vertebrates of any country (The Wilderness Society https://www.wilderness.org.au/articles/australias-biodiversity-summary) and the zoogeographic region Australia holds the phylogenetically most distinct vertebrate assemblage of any zoogeographic region of the world (Holt et al. 2013).

Of the 549 native bird species that breed on the Australian mainland (taxonomy of species follows Garnett et al. (2015), breeding status follows *Handbook of Australian, New Zealand and Antarctic Birds*, Vol. 1–7 (1990–2006)), 83 species (15%) and eight notable subspecies have become extinct, threatened or near threatened since the first Europeans settled in Australia in 1788 (Table 5.1). In almost all of these cases direct and indirect anthropogenic causes are responsible for the decline (Garnett et al. 2011). Habitat alteration is the most frequent such threat (79 of 91 taxa, 87%), followed by predation by introduced carnivores (37 of 91 taxa, 41%). The latter are also considered the major causes of the decline and extinction of Australian native mammals (Woinarski et al. 2015). Non-flying native mammal species in the weight range of 35 g – 5500 g from arid and semi-arid areas are most affected, and 'those confined to the ground's surface are in most danger' (Burbidge and McKenzie 1989, p. 186). Birds, in contrast, are relatively less affected by introduced carnivores (Reid and Fleming 1992), but recent examples affirm that birds, and particularly those that spend much time on the ground, may be severely impacted by that threat (e.g., Priddel and Wheeler 2003). The introduced carnivores referred to are the House Cat *Felis catus*, Red Fox *Vulpes vulpes*, Domestic Dog *Canis familiaris*, and Dingo *Canis lupus dingo* (Dickman 1996, Wheeler and Priddel 2009, Letnic et al. 2012, Frank et al. 2014). All of these, besides the dingo, arrived in Australia with the first European settlers in 1788, or were introduced subsequently (Koch et al. 2015, Spencer et al. 2016). The dingoes are the descendents of a small founder population of domestic dogs that was introduced into Australia about 5000 years ago (Gollan 1984, Savolainen et al. 2004, Ardalan et al. 2012). Dingoes and dogs interbreed when in contact (Newsome and Corbett 1985). Today, the predators mentioned here are widespread across mainland Australia including the arid and semi-arid zones (Figure 5.1). Specifically, their distributions overlap to a considerable extent with that of the rare Grey Falcon *Falco hypoleucos*.

Table 5.1 Threats to the persistence of Australia's bird species and subspecies that breed (or have formerly bred) regularly on the Australian mainland (data taken from Garnett et al. (2011)). Threats include habitat alteration and predation from cats, foxes, and dingoes (and dingo-dog hybrids), and their impact is presented as percentages of species and subspecies affected. The conservation status of taxa follows 'The IUCN Red List Status of Extinct, Threatened and Near Threatened Australian bird taxa', as listed by Garnett et al. (2011).

Conservation status	Number of species	Number of taxa	Number of taxa threatened by habitat alteration	Number of taxa threatened by cats, foxes, or dingoes
Extinct	5	6	100% (n = 6)	33% (n = 2)
Critically endangered	7	7	100% (n = 7)	71% (n = 5)
Endangered	23	26	96% (n = 25)	27% (n = 7)
Vulnerable	20	24	75% (n = 18)	71% (n = 17)
Near threatened	28	28	82% (n = 23)	21% (n = 6)
Total	83	91 [1]	87% (n = 79)	41% (n = 37)

[1] Of some species, more than one subspecies is included.

The Grey Falcon is endemic to the Australian mainland (Chapter 1). Its population is estimated to contain <1000 mature individuals (Schoenjahn 2011a, Garnett at al. 2011, BirdLife International 2016, 2017). The individuals are distributed sparsely over the continent's arid and semi-arid zone (Schoenjahn 2013), which covers about 5 million km^2 (Australian Museum 2002, Pavey and Nano 2006), or about 70% of the Australian mainland. The Grey Falcon is a medium-sized falcon. The body mass of adults captured from the wild ranged from 339 g to 582 g (Chapter 2). Grey Falcons of all ages feed almost exclusively on birds throughout the year (Schoenjahn 2013). They breed no more than once a year, invariably between July and November (Chapter 3).

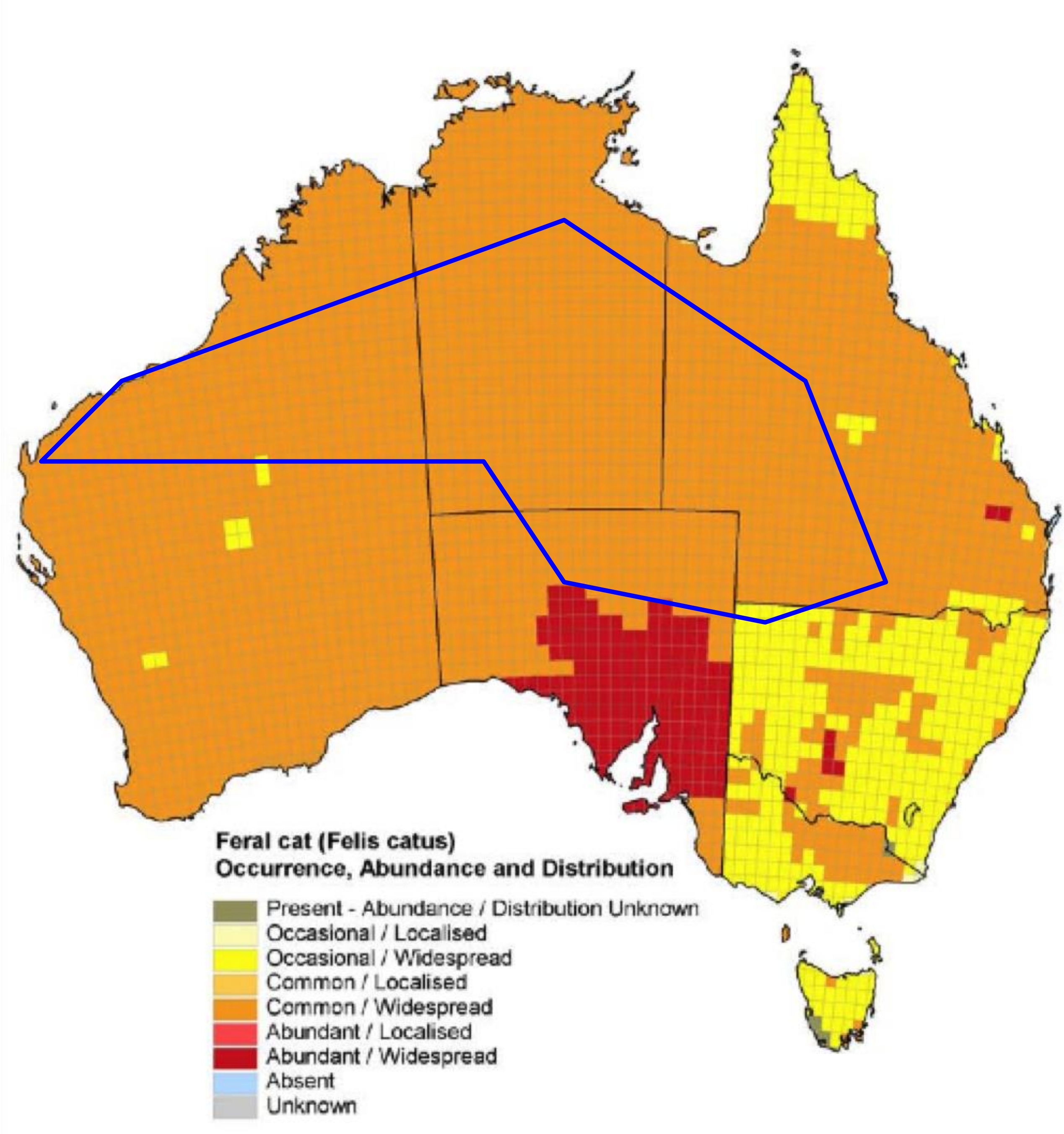
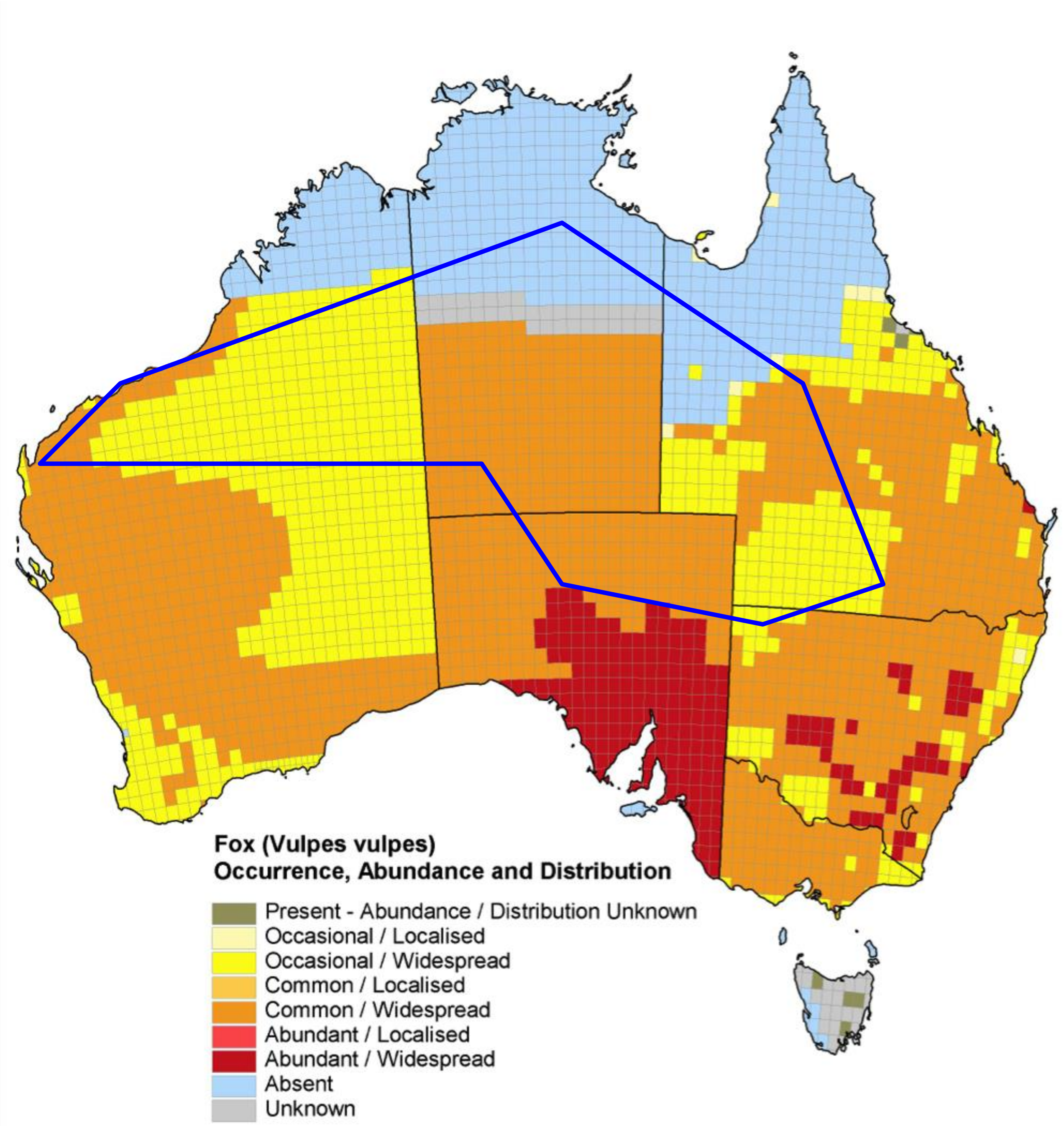


Figure 5.1 Distribution of three alien (eutherian) predators in Australia and the distribution of the breeding records of the Grey Falcon from 2003–2016 (n = 59) (blue polygon). Maps published in (West 2008), and taken from PestSmart https://www.pestsmart.org.au, accessed 12 Nov. 2017. Used with permission.

A) Feral cat

[continued]



B) Fox

Figure 5.1 (cont.)

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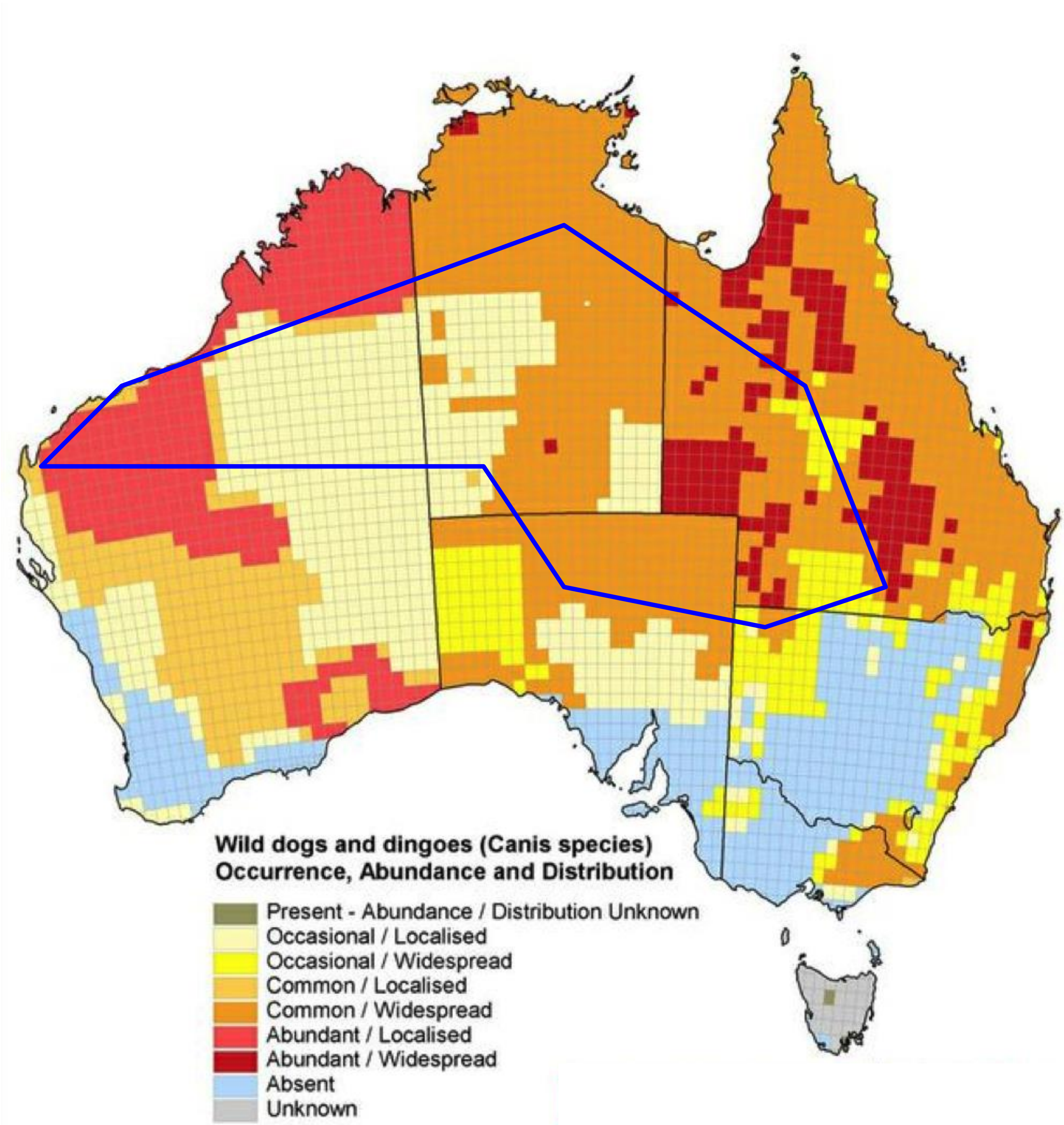

C) Dingo and dog

Figure 5.1 (cont.)

Figure 5.2 Stomach contents of a feral cat, which was shot and dissected in June 2013 in Astrebla National Park, located in south-western Queensland. Note the yellow base of the upper mandible and the bright orange-yellow colour of the leg and toes, all of which are typical for Grey Falcon. The skin of the legs and toes appears fresh and intact and free from marks that would suggest that the Grey Falcon had been dead for some time before being ingested by the cat. Photo courtesy and copyright Maree Rich, Queensland Parks and Wildlife Services, Longreach, Qld.

The Grey Falcon's national conservation status is considered by a number of national and international assessments to be 'Vulnerable', based on the low population size (Garnett at al. 2011, BirdLife International 2016, 2017). Despite wide consensus on the rarity of the species, it is not declared threatened under Australian national legislation, namely the Environment Protection and Biodiversity Conservation Act 1999 (available from http://www.environment.gov.au/, accessed 4 Dec. 2017). However, the conservation status of the species may be re-assessed nationally in 2018 (Professor Stephen Garnett, Charles Darwin University, pers. comm. 21 Dec. 2017).

The Grey Falcon is one of the five rarest species within the genus *Falco* (Schoenjahn 2013). It is also one of its least known because the other four extremely rare species have attracted considerably more research attention. Specifically, the Mauritius Kestrel *F. punctatus* and the Seychelles Kestrel *F. araeus* experienced severe population bottlenecks and were investigated from that perspective (Jones et al. (1995) and Groombridge et al. (2009), respectively), and the Taita Falcon *F. fasciinucha* and the Black Falcon *F. subniger* have been subject to field studies since the 1970s (for summaries see the Global Raptor Information Network, provided by The Peregrine Fund, Idaho http://www.peregrinefund.org/library). The knowledge deficiency with regard to Grey Falcon includes the threats to the species. In the absence of focused studies all propositions regarding threats to the species that have been published are based on general considerations and extrapolations from better studied species and are, therefore, speculative (Garnett and Crowley 2000, Garnett et al. 2011).

In this Chapter I use observational data collected over 15 field seasons to assess the threats faced by the Grey Falcon. This is the first focused study into the threats to the Grey Falcon and the conservation aspects that follow. In particular, I focus on predation by introduced carnivores which was recognized as threat from this study and has not been previously proposed to threaten Grey Falcons. Further, I discuss putative threats that have been proposed by previous authors and those that emerged during the course of fieldwork during this PhD research. Conservation measures to ameliorate threats and to improve the conservation status of the Grey Falcon are proposed.

The chapter is divided into two separate parts. The Methods (5.2) and Results (5.3) sections relate only to ground-roosting (and thus to potential predation by cats, foxes, and dingoes). The Discussion (5.4) considers an assessment of all potential threats to the species.

5.2 Methods

Data from wild Grey Falcons were collected between July 2003 and June 2017. The general fieldwork methods and study area have been described in the previous chapters of this thesis.

After receiving a report (in 2014) that the remains of a Grey Falcon had been found among the stomach contents of a feral cat shot in south-western Queensland (Figure 5.2), I investigated whether Grey Falcons spend much time on the ground; evidence of regular ground-roosting would indicate a vulnerability to cat predation. (That these birds often feed on the ground was reported in the literature referred to in Chapter 1.) Specifically, I examined the satellite-derived tracking data reported in Chapter 4 with regard to whether these birds roost on the ground at night. The satellite tracking method and the analysis of the satellite-derived location data were described in Chapter 4. From satellite tracking of the five satellite tagged Grey Falcons Argos ID 134881, 141276 (NT), 141276 (Qld), 141628, and 150861 (for details of the tagged birds and their transmitters see Chapter 4), a combined total of 843 night-roost locations were obtained (Table 5.2). Most of them (567, 67%) were at localities other than the nest site of the respective individual. Each of the 567 night-roost locations was then plotted on satellite imagery of the earth's surface (freely available from GoogleEarth https://www.google.com/earth/), and the vegetation and topography within 350 m of the location evaluated visually on GoogleEarth. Given the mostly flat and sparsely vegetated landscape in which these birds live, the accuracy of the night-roost locations and the information and resolution of the satellite imagery was adequate to establish with confidence whether the falcon had roosted on the bare ground during a particular night. Specifically, if trees were not discernible on the satellite imagery and the vegetation covered less than an estimated 10% of the ground, I presumed that the bird had roosted during that night on the bare ground.

To establish the precision of the method, I visited seven (5%) of the 149 sites thus identified. These were all at extremely remote locations and were visited within four months of having been used (see Table 5.2 footnotes for examples of the time lag involved). In all cases I found that the vegetation type was similar to what was expected from the satellite imagery. At many other night-roost locations the satellite imagery showed vegetation cover exceeding 10% but without trees. Because I have not observed a Grey Falcon night-roosting on a bush or roosting on a bush at sunset or sunrise (which would suggest night-roosting), it is likely that in those treeless locations the individual involved night-roosted on the ground. Nevertheless, these latter locations were excluded from the count of bare-ground night-roosting and I am, therefore, confident that my method yielded a conservative result.

The severity of a threat is calculated as the product of three parameters: exposure of the individuals to the threat, their susceptibility to the threat, and their adaptive capacity in the face of the threat. In the absence of qualitative information for any of these parameters I use these basic values. Exposure: low, 0; medium, 1; high, 2. Susceptibility: no, 0; yes, 1. Adaptive capacity: no, 1; yes, 0. The resulting values for the severity of the threats range from 0, least concern, to 1, moderate concern, to 2, most concern. This method compares between the severities of threats and gives a relative, not absolute, indication of the threats examined. I acknowledge that in some instances the assigned values are debatable. However, the coarseness of the gradation of each set of values may render the effect insignificant.

Table 5.2 Night-roosting behaviour of five satellite-tracked Grey Falcons. See Chapter 4 for details of the birds and transmitters, and for method of how the approximated locations were obtained from satellite-derived data.

	Bird Argos ID	Frequency of nights during which the individual night-roosted			% Night-roosting on the ground when not at nest
		on the nest-tree or nest-repeater *	elsewhere, i.e. not at the nest	presumably on the ground	
1	134881	29	504	116 [1]	23
2	141276 (Qld)	19	30	10 [2]	33
3	141628	42	7	3 [3]	43
4	141276 (NT)	43	17	12 [4]	71
5	150861	143	9	8 [5]	89
	Total/overall	276	567	149	26

* The bird No. 4 was associated with a nest on a tree but did not breed while being satellite-tracked. The other birds bred (No. 2, 3, 5) or were reared (No. 1) at a nest on a telecommunication repeater tower (Figure 2.1).

[1] On 28 Apr. 2015 the bird night-roosted on the ground at a distance of only about 885 m from the repeater that held its nest, and within sight of it. I verified the vegetation cover *in situ* on 26 Aug. 2015.

[2] The signal became stationary during the night of 26 Dec. 2014, whilst the bird roosted presumably on the bare ground. The location is about 650 m from a timbered creek-line and 770 m from an artificial dam that contained water at the time. I verified the vegetation cover and water level in the dam *in situ* on 25 Mar. 2015. The circumstances suggest that this bird was killed and eaten by a feral cat.

[3] The bird shed the transmitter and harness on 7 Jan. 2015, the day on which the signal was lost, and was seen in company of its partner thereafter. See Chapter 4 for further details.

[4] The signal became stationary at a location at an inter-dune swale in the morning of 1 Jan. 2016. The bird died of unknown causes. I presume that it spent its last night roosting on the bare ground at that location. I retrieved the remains of the bird and verified the vegetation cover *in situ* on 18 Mar. 2016.

[5] The last signal was received on 5 July 2016 at 0313 hr LST (local solar time, see Chapter 2 for definition) from a location at an inter-dune swale, whilst the bird night-roosted presumably on the ground. I verified the vegetation cover *in situ* on 3 Oct. 2016. The high incidence of this individual roosting on the ground during nights spent away from the nest, eight (89%) out of nine nights, may be partly explained by the circumstance that the nest was in a sand-dune desert location with very few trees. The circumstances suggest that this bird fell prey to a cursorial predator while roosting at night on the bare ground.

5.3 Results

A third of all night-roosts identified (276, 33%, n = 843) involved the bird's nest site, and the remainder (567, 67%) were at other locations (Table 5.2). Of the latter, 26% (149) were on the bare ground. The locations of all night-roosts fall within the current distributions of feral cats and dingoes (and dingo-dog hybrids), and overlap to a large extent with that of the fox (Figure 5.1).

Remains of a satellite-tagged adult Grey Falcon (Argos ID 141276, see Table 4.2) were found in south-west Queensland's Channel Country on 25 Mar. 2015 (frontispiece, photo 'F'). Circumstantial evidence *in situ* suggested that the bird, while roosting on the ground at night, was killed and eaten by a feral cat. That is, it appeared that the falcon was eaten in a small opening in the base of a dead thorny bush, with the opening being too small to admit a fox.

Potential threats to Grey Falcon individuals, and the species as a whole, are listed in Table 5.3, and the records of Grey Falcons found injured or dead along roads are collated in Table 5.4 as an indication of the threat posed to these birds by traffic. The current relative severity of each threat is calculated, in Table 5.3, as the product of the values assigned to the parameters "exposure", "susceptibility", and "adaptive capacity". All threats listed are, directly or indirectly, anthropogenic with the exception of the threat 'small population size', a threat that falls in the category 'least concern'. The actions listed are the conservation measures proposed to alleviate the corresponding threat to the Grey Falcon.

5.4 Discussion

An important and hitherto unidentified threat to the Grey Falcon derives from this study: predation from feral house cats. This threat is the consequence of the unusual and unexpected behaviour of these birds to regularly night-roost on the ground which exposes them to predation by these terrestrial carnivores alien to Australia. Further, I suggest that, in the same way, the Grey Falcon is potentially threatened by introduced red foxes and dingoes (and dingo-dog hybrids).

Table 5.3 Possible threats to individuals of Grey Falcon and the species as a whole, the relative potential severity of the threat with regard to the possible extinction of the species, and the actions proposed. 'Prev. nom.', a previous author nominated it as a potential threat; 'Expo.', exposure of the individuals of Grey Falcon to the threat; 'Sus.', susceptibility of the individuals to the threat; 'Adap.', adaptive capacity of the species in the face of the threat (note that the value '1' indicates a lack of adaptive capacity). For the definition of values see text. '?', the value of the parameter is unclear, further studies are required. 'Unclear', one of the three parameters is unclear.

	Threat	Prev. nom.	Evidence and/or reference	Expo.	Sus.	Adap.	Relative severity of threat	Conservation measures (and further research) proposed
1	Introduced carnivores	No	This study.	2	1	1	**Most concern**	Suppress feral cats, foxes, and dingoes in the arid zone.
2	Climate change	No	This study. Speculative	1	1	1	Unclear, assumedly increasing	Globally combat climate change. Further research into the species' ecology and, particularly, physiology.
3	Small population size [1]	Yes	Schoenjahn (2013) and this study.	1	1	0	Least concern	None.
4	Habitat alteration [2]	Yes	Speculative. Garnett et al. (2011)	1	?	1	Unclear	Suppress feral camels (see footnote [2], and text).
5	Nest shortage	Yes	Speculative. Garnett et al. (2011)	?			Unclear	Retain telecommunication towers in the arid zone. Evaluate replacement rate of suitable nest trees.
6	Bird watchers, photographers	Yes	Watson (2011) Pedler (2016)	0	1	1	Least concern	Keep nest locations strictly confidential. Promote ethical behaviour at nests: visits ≤ 30 min, distance ≥ 300 m, no repeat visits by, e.g., tour operators, no publishing of photos of active nests.
7	Collision with traffic	No	Table 5.4. This study.	0	1	1	Least concern	None.
8	Collision with fences and power-lines	Yes	Schoenjahn (2011b)	0	1	1	Least concern	Dismantle or collapse decommissioned fences in the arid zone.
9	Egg collecting	Yes	Speculative. Garnett et al. (2011)	0	1	1	Least concern	Maintain and enforce existing laws and regulations.
10	'Harvesting' for falconry [3]	Yes	This study. Brouwer and Garnett (1990)	0	1	1	Least concern	Maintain and enforce existing laws and regulations.

[1] Threats as a result of small population size include stochastic environmental events and inbreeding (Frankham and Ralls 1998, Saccheri et al. 1998). See text.
[2] Includes indirect anthropogenic causes, particularly habitat alterations by introduced herbivores, such as feral Arabian Camels *Camelus dromedarius* (Garnett et al. 2011, Jupp et al. 2015).
[3] 'Harvesting' refers to the take of live birds or fertile eggs from the wild.

Table 5.4 Records of Grey Falcons found injured or dead along roads as an indication of the risk that traffic poses to Grey Falcons. 'NP', National Park.

	Date	Approx. location	Circumstances	Remarks
1	June 2007	White Cliffs, NSW	Found by NP rangers on roadside. Died in care after a few days.	Now at Australian Museum (Schoenjahn (2011b).
2	June 2009	Port Headland, WA	Found by motorists along highway. Permanently damaged wing.	In care at Eagles Heritage, WA (Schoenjahn 2011b).
3	Sep. 2010	Jundah, Qld	Found by me on main road in township. Dead since two or more days, partly decomposed.	This study.
4	2013	Karijini NP, WA	Juvenile, flew into a moving truck and got stuck in the horn.	Released after rehab. [1]
5	May 2016	South Hedland, WA	Found by motorists along highway. Minor injury, released after rehab., satellite-tagged.	Bird Argos ID 150860, see Chapter 4.
6	Feb. 2017	Paraburdoo, WA	Found by motorists along country road. Died from injuries while in care.	Now at WA Museum.

[1] A. Tonndorf (wildlife carer at Tom Price, WA), pers. comm. 12 May 2015. I determined the species and age of the individual from photos provided by A. Tonndorf.

In addition, I propose that the Grey Falcon is vulnerable to the effects of climate change. That is, the climatic changes that are expected for Australia have the potential to affect the species by way of exceeding its physiological and behavioural capacities of coping with extreme weather, and by causing a change to its distribution (e.g., fragmentation or shift to higher latitudes). Climate change may, therefore and ultimately, threaten the species as a whole.

In this section I present and discuss the putative threats to the species that emerged from this study and those that were mentioned by previous authors. Further, I evaluate, in Table 5.3, the severity of each threat relative to the other threats examined here, and I also suggest conservation measures.

Introduced carnivores

The threat of predation from feral cats is a consequence of the Grey Falcons' behaviour to roost often on the ground at night. Specifically, the satellite-tagged birds roosted on the ground during 26% (149, n = 567) of the nights that they spent away from the nest, and presumably night-roosted on the ground even more frequently. This behaviour evidently exposes these birds to predation by feral cats, and, potentially, other carnivores alien to Australia, namely foxes, and dingoes (and dingo-dog hybrids). These carnivores have all arrived in Australia only recently in evolutionary terms (see above).

I argue that Grey Falcons are naïve to these predators. To accept this one has to appreciate two points. (i) The Grey Falcon is thought to have diverged from its closest relative about 1.4–2.8 million years ago (mya) (Fuchs et al. 2015), i.e. during the Quaternary (~2.6 mya to present). (ii) The two autochthonous cursorial predators of the Quaternary on the Australian mainland that were large enough to kill a Grey Falcon, the Thylacine *Thylacinus cyanocephalus* and the Tasmanian Devil *Sarcophilus harrisii*, are believed not to have occurred in the arid zone (Archer 1974, Dawson 1982), which is the core breeding distribution of the Grey Falcon (Schoenjahn 2013).

Today, in contrast, feral cats, foxes, and dingoes are relatively common in the arid zone (Figure 5.1). These species are opportunistic ambush-hunters that stalk their prey (Paltridge 2002, Spencer et al. 2016, Mella et al. 2017). Feral cats, for example, hunt most successfully in open environments (McGregor et al. 2015), i.e. typical environments of the Grey Falcons' on-ground night-roost sites. The circumstances of the deaths of the Grey Falcons No. 2 and 5 in Table 5.2 appear to affirm the reality of this threat.

Present-day autochthonous terrestrial predators able to kill a Grey Falcon are snakes (Suborder Serpentes) and monitor lizards (Family Varanidae). Monitors are strictly diurnal and present, therefore, no threat to a night-roosting Grey Falcon (Cogger 2000). Snakes large enough to kill and, importantly, swallow prey of Grey Falcon size include large individuals of the largest terrestrial species, and particularly pythons (Family Boidae) (Shine 1977, 1991, Slip and Shine 1988, Bryant et al. 2012). Further, in snakes, a major factor in locating, attacking and swallowing prey is the sensory information from the Jacobson's organ (vomeronasal system) which enables them to track non-volatile chemical cues ('scent'-trails) (reviewed by Halpern (1987); also Young (1990)). The tracking of volatile chemical cues by means of the nasal apparatus seems to be of lesser importance (Burghardt 1970, Halpern 1987). Further, snakes may also locate their prey by sensing ground-borne vibrations generated by moving prey (Friedel et al. 2008). In consequence, snakes appear unlikely to frequently locate birds that sleep on the ground at or very near the spot where they alighted. Therefore, the predation pressure from snakes on the Grey Falcon appears to be of little significance.

In summary, it appears that before the arrival of the alien predatory mammals cats, foxes, dingoes and dogs, Australia's arid zone was free of predators that would habitually take a Grey Falcon on the ground at night. In consequence, the Grey Falcon can be considered naïve to predation by these carnivores.

Evidently, Grey Falcons are exposed to this threat at all times and throughout their distribution. Feral cats, foxes, and dingoes take a large variety of vertebrate prey, and, particularly in the arid zone, birds (Paltridge 2002). Feral cats exert, perhaps, the greatest threat to the Grey Falcon because of their overlapping distribution, the high density of cats, and because the cats' diet has the highest proportion of birds among the mammalian predators concerned here (Woinarski et al. 2017). Specifically, feral cats occur throughout the Australian mainland, their population fluctuates between 2.1 and 6.3 million, and densities may, under exceptional circumstances, reach 750 cats/km^2, and up to 2000 cats/km^2 where food is particularly plentiful (Liberg and Sandell 1994, Denny et al. 2002, Legge et al. 2017). Feral cats alone are thought to kill 272 million birds per year in Australia's natural (i.e. non-urban) landscapes (Woinarski et al. 2017). Importantly, with regard to Grey Falcon, bird-kill rates of feral cats are particularly high in Australia's arid zone, and medium-sized birds (i.e. body mass 60–300 g) that spend considerable time on the ground are most likely to be taken (Woinarski and Murphy 2017). Being opportunistic hunters, feral cats, foxes, and dingoes can be expected to use every single opportunity to kill a Grey Falcon sleeping in the open on bare ground.

The impact that of the threat from introduced carnivores on the population of the Grey Falcon remains unquantified and, in the case of fox and dingo, hypothetical. Evidently, however, the threat from feral cats is acute and its omnipresence suggests that it has the potential to impact significantly on the longevity of the Grey Falcon as a species.

Climate change

I propose that climate change has the potential to threaten the Grey Falcon. This is a consequence of the species remaining at all times in the arid/semi-arid zone, a hot environment characterized by extreme and unforeseeable climatic events. Specifically, the predicted increases in severity and frequency of days with very high temperatures, heat waves, droughts, and deluges of rain, may exceed the physiological and behavioural capacities of these birds to thermoregulate adequately.

Climate predictions for the immediate and mid-term future foresee increases in maximum temperatures and increases in frequency, amplitude and duration of extreme climatic events (Meehl and Teribaldi 2004, Suppiah et al. 2007, Moise and Hudson 2008, Head et al. 2014). Changes expected to be most relevant to native animal species that inhabit Australia's arid and semi-arid zones were identified in a study by Pavey (2014), involving an area that comprises much of Australia's arid and semi-arid zones and, therefore, much of the Grey Falcon's breeding distribution. The results are listed in Table 5.5. Birds were, however, predicted (together with frogs) to be the least impacted taxonomic group among plants and animals in that region (Pavey 2014). Despite the prediction of least impact for birds as a group, the Grey Falcon emerges as a species that may well face increased environmental stress as a consequence of the predicted changes in climate. The species may already experience elevated environmental stresses as a result of recent changes in climate. Increasing environmental stresses increase the extinction risk (Colinvaux 1973). Therefore, the concern for the future of the Grey Falcon arises from the increase of the severity and frequency of extreme climatic events, including extremely hot days, heat waves, and deluges of rain (Jentsch et al. 2007, Watterson et al. 2015). These changes challenge the Grey Falcon physiologically and behaviourally.

Table 5.5 Summary of the predicted changes in a range of climate variables within the Rangelands Cluster National Resource Management region by 2090. **Bold** indicates the changes of most importance when considering impacts on native species. Taken from Pavey (2014, p. 5).

Climate variable	Projected change
Temperature	**Increase in all seasons**
Extreme temperatures	**Increase in hot days**, decrease in cold days
Rainfall variability	**Remain high**
Extreme rainfall events	**Increase in intensity and frequency**
Winter and spring rainfall	A decrease more likely than an increase
Summer and autumn rainfall	Trend is unclear
Potential evapotranspiration	**Increase in all seasons**, most strongly in summer

Physiologically, Grey Falcons appear to posses the same characteristics as most bird species (Chapter 2). To cope with the severity and frequency of the extreme climatic events that characterize their environment, Grey Falcons presumably depend on a relatively fine balance between gaining heat from the environment and their own metabolism during physical activity, and minimizing endogenous heat gains by keeping activity levels low (Chapter 2). Any further increase in the severity and duration of periods of extreme heat loads may result in the physiological and behavioural capacities of these birds being exceeded more frequently than at present. This may be illustrated by the following observation. On a day with temperatures above 50ºC and strong wind, a fledgling Grey Falcon was found dead beneath a nest with a second fledgling on the ground unable to fly (Schoenjahn 2011b). Evidently, there is a limit to the heat load with which nestlings can cope, and this is, arguably, true for Grey Falcons of any age (for birds in general see Towie (2009)).

The humidity of the Grey Falcon's current environment is also predicted to increase, and is, perhaps, currently already increasing (Table 5.5). That is, the evapotranspiration in that area is likely to increases in all seasons, and this can be expected to raise the relative humidity in the arid zone generally. Elevated humidity is suggested to be responsible for excluding Grey Falcons from more mesic areas (Chapter 2). This is because moisture in the air hampers evaporative cooling and helps to conduct heat, and may, therefore, lower the heat load these birds can tolerate.

The changes predicted for the climatic conditions in areas where Grey Falcons are presently found may change the distribution of these birds. Distributional changes may include (i) a gradual geographic shift toward higher latitudes on the Australian mainland because climates there may become similar to what Grey Falcons experience at present, and (ii) a contraction or fragmentation of the distribution because suitable climates can be expected to become less widespread than at present.

In summary, the individuals of Grey Falcon are clearly exposed to the changes expected from climate change and they appear to be susceptible to these changes, and notably to those that increase the heat loads to which these birds are exposed. Their physiological and behavioural capacities to cope with these changes are, evidently, limited. In consequence, the Grey Falcon is vulnerable to climate change (*sensu* Dawson et al. 2011) in the immediate and mid-future.

Small population

A threat to the species as a whole lies in its extremely small population size, estimated at <1000 mature individuals. Indeed, small populations are expected to have an increased probability of extinction compared to large populations (i.e., populations as large as and exceeding 1,000,000 individuals) (Gillespie 2001) because of the relatively higher impact of stochastic processes, and, possibly, inbreeding (Frankham and Ralls 1998, Saccheri et al. 1998, Traill et al. 2010). For this reason, small population size is a criterion in assessments of conservation status for the IUCN Red List (http://www.iucnredlist.org/static/categories_criteria_3_1). The minimum census size for populations to be genetically viable in perpetuity has been suggested to be, in general, 5000 individuals (Traill et al. 2010). However, this number is a generalization and it is unclear if the minimum census size is applicable to populations that are, such as that of the Grey Falcon, spread at extremely low density across a vast area. The mobility level and movement patterns of the individuals of such a small population may be of pivotal importance. At any rate, the Grey Falcon's population size of less than 1000 individuals causes concern. Here I identify and discuss aspects of this concern and I also comment on the possible causes of the low densities of Grey Falcons.

The stochastic processes referred to above include catastrophic environmental events and disease epidemics. Both processes are most effective when a significant portion of the individuals of the population in question occur in an area small enough for all individuals to be simultaneously affected by the catastrophe. From the Grey Falcon's low density across a vast area it follows that stochastic processes are, despite the species' small population, unlikely to pose a significant threat.

Inbreeding increases the frequency of homozygosity in a population, including homozygosity that involves deleterious alleles, and may also reduce the genetic variation present within a given population (Lerner 1954, Traill et al. 2010, Luo et al. 2015). This risk is especially critical in cases of extreme inbreeding, involving parent and offspring or siblings. However, evidence for inbreeding depression (i.e. the reduced biological fitness in a population as a result of inbreeding) from natural populations of nonhuman animals is scant, and that includes birds (Gibbs and Grant 1989, Hoogland 1992). Nevertheless, the Grey Falcon seems to have some potential for inbreeding. The population is small, and parents and offspring, or siblings, stay together for up to 12 months or longer, i.e. until the young reach reproductive age. Examples of a single parent being found in close association with a single one-yr-old presumed offspring of the opposite sex are Numbers 17, 19, 20, and 21 in Table 3.2 (Chapter 3). Further, two yearlings, presumably siblings, were photographed together on 18 July 2012 in South Australia (R. Clemens, School of Biological Sciences at The University of Queensland, pers. comm. 25 July 2012), and two yearlings were found together on 18–19 Oct. 2009 (Schoenjahn, pers. obs) at a 2008 nest site in Queensland (No. 5 in Table 4.6). However, Grey Falcons have been shown to conduct wide-ranging movements of up to, and almost certainly in excess of, 280 km in one day and 1000 km within eight days, with one of the putative purposes of these expansive excursions being mate seeking (Chapter 4). Further, the species is considered to consist of a single panmictic population (Garnett and Crowley 2000) with no evidence to the contrary. This perception is supported by the analysis of the mitochondrial Cytochrome *b* gene region extracted from feathers that I collected during this study from 26 individuals of Grey Falcon across the species' entire distribution (Mullin 2017). Haplotype diversity was relatively high and all haplotypes were widespread. In summary, I assume that inbreeding in the Grey Falcon is not particularly high and inbreeding effects are insignificant.

It thus appears that small population size is unlikely to be an immediate threat to the Grey Falcon. The extremely large distribution of Grey Falcons and the mobility of the birds may help the species to persist. That is, these bird can evade adverse conditions that may affect parts of the species' distribution but which would be unlikely to affect its entire distribution. Further, the species' high level of mobility helps to combat evolutionary challenges through the potential to interbreed randomly across the entire population and, thus, compensate for losses of genetic variation by gains through mutation, i.e. losses that may reduce the population's ability to respond to future environmental changes (*sensu* Lande 1988, Frankham 1995). Despite its low-density distribution, the Grey Falcon persists at that level with no evidence of a decline detected since the species became known to science in 1839 (Marchant and Higgins 1993, Schoenjahn 2010a, Garnett et al. 2011, Schoenjahn 2013).

With regard to explaining the small size of the Grey Falcon's population observed today, at least three alternatives are possible. (1) The species has always been rare. (2) The species is currently in a quasi-stable pre-extinction period and is declining slowly toward extinction (*sensu* Kemp 1985, especially p. 64, Fig. 1). (3) The species is currently going through a temporary population bottleneck. The alternatives (2) and (3) lack evidence, as mentioned. For example, quantitative information necessary to recognize population trends is unavailable. New information is, however, emerging from DNA analysis (Mullin 2017). The results of that study add support to the view that the species has not experienced a recent population bottleneck, suggesting rather that the species has been rare for tens of thousands of years.

Habitat alteration and nest availability

'Clearance of the semi-arid zone for marginal farming' and 'overgrazing of the arid zone rangelands' (Garnett and Crowley 2000, p. 196, also Garnett et al. 2011) have been named as possible threats to the Grey Falcon for their potential to affect the availability of trees for nesting (Grey Falcons nest exclusively in stick-nests, Schoenjahn (2013)), and to reduce prey abundance.

In regard to the availability of trees, information is needed that evaluates the replacement rate of suitable nest trees in Australia’s arid and semi-arid zones. The threat appears to stem mainly from domestic livestock (cattle and sheep) and introduced (feral) goats *Capra hircus* and rabbits *Oryctolagus cuniculus* destroying existing vegetation and hampering the growth of new trees (Auld 1990, 1995, Mutze 2016). In regard to the general availability of suitable nests, one must appreciate that Grey Falcons use the existing nests of other species exclusively, in line with its congeners (Brown and Amadon 1989). Grey Falcons use, predominantly, the nests of corvids (genus *Corvus*) (Olsen and Olsen 1986, Schoenjahn 2013). The combined distribution of the three corvid species Australian Raven *Corvus coronoides*, Little Crow *C. bennetti*, and Torresian Crow *C. orru* covers the Grey Falcon’s breeding distribution, and all three corvids are common within their respective distribution (Blakers et al. 1984, Barrett et al. 2003, Higgins et al. 2006, Schoenjahn 2013). Further, the populations of all three corvids are currently increasing rather than decreasing, and this holds also for the arid zone (Higgins et al. 2006). Nonetheless, not all nests built by these corvids are suitable for Grey Falcons because the latter favour nests in the highest part of the highest tree available, whereas corvids may build their nests also in, for example, 4–5 m tall bushes (Schoenjahn, pers. obs.). Therefore, as long as suitable trees are available, suitable nests can be expected to be sufficiently available. Further studies into the replacement rate of suitable trees are warranted.

Of particular interest in this regard is the observation that most nests found during this study (29, 73%, n = 40) were on artificial structures, including repeater towers (24, 60%, n = 40), some of which have been decommissioned for decades (Schoenjahn, unpublished data). Nesting on these tall structures has advantages to the Grey Falcons, including safety from terrestrial predators and, presumably, ants (for the threat from ants see Higgins (1999, p. 838), and Ricklefs (1969)). Retaining the decommissioned telecommunication repeater towers in Australia’s arid and semi-arid zone will, presumably, benefit the Grey Falcon.

In regard to grazing affecting prey abundance, field observations suggest that that Grey Falcons hunt predominantly in open country, often over treeless grassland, which is also a key feeding habitat of the prey species recorded (Schoenjahn 2013, and Chapter 4).

In addition, Grey Falcons are well known for hunting at natural and artificial watering places (Smith 1983, Baumgart and Baumgart 1998, Silcocks 2007, Schoenjahn, pers. obs.). Therefore, the Grey Falcon may in fact benefit from grazing (not overgrazing) and the provisioning of artificial watering places. In regard to natural watering places, they may be more numerous than assumed ‘by the white man’ (Thomson 1962, p. 270, Bayly 1999, Jupp et al. 2015, especially Figure 3). However, natural watering places in the arid zone are known to get destroyed or depleted by feral Arabian Camels *Camelus dromedarius* (Garnett et al. 2011, Jupp et al. 2015, Brim Box et al. 2016). Therefore, the susceptibility of the Grey Falcon to the threat from habitat alteration remains speculative, notwithstanding that the species may benefit from a reduction of the numbers of feral camels.

Bird watchers and photographers

The Grey Falcon is a highly sought after species by bird watchers and bird photographers. In consequence, nest sites of the species are visited by casual birders and commercial bird tour groups during the breeding season in the hope to see the species. Some sites of active nests have been publicized online (e.g., Watson 2011) which led to a number of people visiting the respective site while the birds were breeding. Ethical birding, as promoted now by many bird watching and photographing organizations (e.g., Australian Birdlife http://www.birdlife.org.au/documents/POL-Ethical-Birding-Guidelines.pdf, Audubon Society http://www.audubon.org/get-outside/audubons-guide-ethical-bird-photography), is strongly encouraged.

Collision with traffic and fences

Grey Falcons spend considerable time on the ground, often feed themselves and dependent young on the ground, and this includes the sides of roads and tracks (Chapter 1). In consequence, these birds collide with moving traffic, and casualties have been reported (Table 5.4). Although the threat from traffic appears small at present, the threat is obviously on the increase because the network of roads and tracks in the arid zone of Australia is, if only slowly, increasing, in line with other parts of the world (Ibisch et al. 2017). Measures to protect Grey Falcon individuals from becoming traffic casualties appear to be non-existent. Similarly, Grey Falcons have been reported receiving life-threatening injury from colliding with fences, and presumably power-lines (Schoenjahn 2011b). Fences, however, could be dismantled once decommissioned. Nevertheless, the current density of roads and, presumably, fences in the distribution of the Grey Falcon is considered very low (for road density see Ibisch et al. (2017)). In consequence, collision with traffic and fences seems to be an inevitable threat to the Grey Falcon, but may be considered minimal.

Egg collecting and falconry

Egg-collecting was undoubtedly a threat until about the late 1980s (Cupper and Cupper 1981, Dennis 1986, Hollands 1984, SAOA 1992), but may not be of such importance any longer because collecting and possessing eggs and empty egg-shells without a permit is now illegal in all Australian states and territories.

The species' potential for falconry was suggested early, by Gould (1865). Although illegal in Australia, the international demand from falconry for rare falcon species and colour morphs appears to be strong (for examples see Booms (2012), ABC (2016)). Indeed, the illegal wildlife trade is considered the second-largest black market worldwide, after narcotics (Toledo et al. 2012, Low 2015). Unfortunately, the findings of this study may increase the vulnerability of the Grey Falcon to illegal activities by making it easier than before to locate individuals in the wild. However, the species' hunting behaviour, especially the tendency to give up on a targeted prey when failing to capture the latter at even the first attempt (Table 2.3), may render it unsuitable for falconry. Regardless, I am unaware of Grey Falcons being trafficked out of Australia and it has been hinted to me that the rigors of the Australian Customs Authorities are to 'blame'.

In summary, I assume that the threat to the Grey Falcon species as a whole from illegal activities is, at present, minimal.

Insecticides

The organochlorine DDT was used as an insecticide in Australia from 1942. The substance caused egg-shell thinning in some Australian species of *Falco* (Olsen and Olsen 1985). The Grey Falcon was also claimed to have been affected but to a marginal extent compared to the Peregrine Falcon *F. peregrinus*, which was most effected (Olsen and Olsen 1985). However, this claim was based on the analysis of the identical samples that were used in the study of Olsen and Olsen (1986), and these samples have been shown to include clutches from other species (Schoenjahn 2013). At any rate, the use of DDT was banned in Australia in 1987 and it is presumed that the effects of that substance are not now felt on the Grey Falcon. The threat was disregarded by Garnett and Crowley (2000) and Garnett et al. (2011), and is likewise disregarded here.

5.5 Conclusion

This is the first focused study on the threats to the Grey Falcon, and the first study to propose conservation measures for that species that are based on a focused study. The main threat appears to be predation by feral cats. Further, foxes and dingoes (and dingo-dog hybrids) also have the potential to prey on, and thus threaten, the Grey Falcon, but evidence is wanting. The effects of climate change, which are predicted to increase in the near to mid-term future, may also have the potential to threaten the Grey Falcon (climate change being projected to, perhaps, become the most significant cause of species extinction (Dawson et al. 2011, p. 53)). The identification of these apparent respectively potential threats is an unexpected result of this study.

In summary, the prime conservation recommendation is to suppress feral cats in Australia’s arid zone.

I hope that this first focused investigation into, and classification of, the potential threats to the Grey Falcon provide a starting point for future studies into the unusual ecology of the Grey Falcon and further yet unknown processes that affect this and other organisms that persist in Australia’s arid zone.

Chapter 6

Summary and synthesis

6.1 Introduction

The Australian fauna has a disproportionate number of species with extremely unusual morphology and behaviour. Examples are the Spotted Handfish *Brachionichthys hirsutus*, a benthic fish that 'walks' on four hand-shaped fins rather than swims (Australian Museum https://australianmuseum.net.au/), the Platypus *Ornithorhynchus anatinus*, an aquatic mammal with a duck-like bill that lays and incubates eggs and suckles its young and in which the male is poisonous (ibid.), kangaroos (Marsupialia, genus *Macropus*) that can delay the development of an embryo (embryonic diapause) until the previously born young is nearing the end of its pouch-life or dies or is abandoned (Nowak 1991), and the Letter-winged Kite *Elanus scriptus*, the world's only truly nocturnal species among the generally diurnal raptors that make up the order Falconiformes (del Hoyo et al. 1994). Indeed, the Australian zoogeographic region holds the phylogenetically most distinct vertebrate assemblage of any zoogeographic region of the world (Holt et al. 2013).

The rare Australian endemic Grey Falcon is a fitting member of that assemblage, as this first autecological study on the species has revealed. When this study commenced in 2003, the Grey Falcon's ecology was little known and it was generally treated as a typical falcon that moved in and out of the arid zone as conditions changed seasonally. However, the information available was limited and derived almost entirely from opportunistic observations and material in museum collections (Schoenjahn 2013). Information was available only on the species' occurrence, movement patterns, diet, and breeding cycle, and was based largely on anecdotal observations and, sometimes, second hand reports. Statements and perceptions were, however, often questionable or contradictory.

The difficulty in finding these rare birds (with an estimated global population of <1000 individuals), distributed thinly across much of Australia's arid/semi arid zone (which comprises ~5 million km^2), impeded detailed studies, and especially long-term investigations. This difficulty is reflected in this study in, for example, the lack of breeding records for the three consecutive breeding seasons 2004–2006 (although breeding was subsequently shown to have occurred in 2006 (Chapter 3)).

During the preliminary phase of this study, 2003–2013, my observations indicated strongly that the species is restricted to the hot arid and semi-arid zones of Australia, which are characterized by extreme and unpredictable climatic events. Further, I suggested that climate is an important factor in explaining the species' scarcity (Schoenjahn 2013). To understand the processes that help the species to survive in that extreme environment, I explored in this thesis key aspects of the species' ecology, morphology, and anatomy, and examined whether these aspects are of significance with regard to the persistence of the species in its extreme environment.

6.2 Summary of significant findings from this research

Low day-to-day activity levels across the year

Grey Falcons keep activity levels low in each aspect of their day-to-day lives, and thus reduce physical exertion (Chapter 2). This contrasts strongly with the general image of the true falcons (e.g., Peregrine Falcon (Cade 1982, Sherrod 1983)). At the same time, these birds appear to lack particular morphological or physiological characteristics that would allow them to cope with heat better than other birds do, with the possible exception of the proposed early thermoregulatory capacity of the young Grey Falcons (Chapter 2). Because the behaviour of these birds in keeping day-to-day activity levels low was consistent across all individuals of the species independent of the geographic location in which they were observed and the time or season of the year, this behaviour can be considered a species-specific adaptation to their environment, one of the hottest and most extreme environments in the world. A possible explanation is that low activity levels help to keep endogenous heat production low and thus enable these birds to respond to any immediate needs and to extreme and unexpected environmental changes completely and without delay.

A potential trophic response of a species that is restricted to a specific environment is to have a broad diet that enables individuals to switch among food types across time depending on their availability. In contrast to this prediction, Grey Falcons of all ages and at all times feed virtually exclusively on flying birds within the body-mass range of 12–300 g (Chapter 1). This high protein food may require fewer hunts to satisfy their daily energy demands and thus reduce the heat-gain from physical activity. Further, Grey Falcons seem to gain all their dietary water from their food. In consequence, I propose that their restricted diet helps the Grey Falcons to persist in the arid environment of inland Australia.

To further clarify this point, the energy budgets and body temperatures of individual birds would need to be assessed. Both aspects appear, however, very difficult to investigate. That is, the assessment of an individual's energy budget and food intake requires the observer to monitor the individual uninterruptedly for useful periods, which is impeded by the extended trips that these birds undertake across terrain often inaccessible to the observer, and the measuring of body temperature, typically requiring invasive methods (McCafferty et al. 2015), may fail to get animal ethics approval.

Extended juvenile dependence

The extended juvenile dependence in Grey Falcons is without parallel among species in the genus *Falco* and other raptors of similar size (Chapter 3). It is typical for young Grey Falcons to stay with their parents in a close family group for up to 12 months and more after fledging. In only one (3%) of 39 independent records of one or more Grey Falcons that involved at least one juvenile at the age of 5–12 mo after fledging it seemed that the juvenile involved (No. 7 in Table 3.3, aged about 10 mo after fledging) was not closely associated by a parent. Even at this advanced age of the young, the adults almost invariably showed no signs of aggression toward them and fed them (*contra* to other species of *Falco*). The key survival skills of these 1-yr-old birds were clearly well below the standard that typifies the behaviour of adult birds, including flying and food handling. Significantly, 1-yr-old birds were occasionally fed piecemeal by their parents, i.e. in the same way in which nestlings and newly-fledged young are fed. This feeding occurred even in the exceptional cases that the parents were breeding in the subsequent season. Further, the young birds were never encouraged to practice behaviour associated with hunting, as are other *Falco* young at this age. It thus seems that young Grey Falcons must learn to keep activity levels low. As outlined in Chapter 3, I interpret the slow skill development and the consequential extremely extended dependence of the young Grey Falcons as a consequence of the behaviour of Grey Falcons of all ages to keep activity levels low at all times.

Reluctant nomadism

Grey Falcons have a unique approach (at least among Falconiformes) to interacting with their environment, which I term 'reluctant nomadism' (Chapter 4). Individuals or pairs of the species remain in an area for some weeks or months, or even as long as two or (rarely) three consecutive breeding seasons, and only then shift to a new area. The new and likewise temporary area may overlap in part with the previous area or it may be disjunct and distant from it. The species' behaviour is, therefore, generally nomadic, as has been suggested by the data from the few available long-term bird surveys that included the Grey Falcon. However, this study showed that these birds even remain in an area if conditions become inadequate for breeding. They rather forego breeding and stay than embark on a risky search for more favourable conditions that may be far away. This suggests that they move on only when environmental conditions become a risk to their survival, i.e. only when absolutely necessary, and when they do move on, they move no farther than necessary. The nomadic behaviour of these birds has, therefore, a distinct element of reluctance.

From the Grey Falcon's strong specialization on birds within a particular size range (Schoenjahn 2013), many of which are nomadic and may occur also outside the arid zone (Chapter 1), it may be expected that the movements of the Grey Falcons would be governed by the nomadic movement of their prey species, i.e. that Grey Falcons would be similarly nomadic. However, the movement patterns of the Grey Falcon uncovered by my study confirm it is a reluctant nomad that rather foregoes breeding than follow favourable conditions, and that the species remains within the arid/semi-arid zone at all times. This pattern does not fit that of a predator tracking the nomadic movements of its primary prey populations.

The movement pattern 'reluctant nomadism' of the Grey Falcon may be seen as being in line with the species' general behaviour of keeping activity levels low at all times.

Night-roosting on the ground

Grey Falcons often roost on the bare ground at night in locations lacking trees or shrubs (Chapter 5). This behaviour was unexpected despite the species being known to roost and feed on the ground during the day. The species also often even feeds young on the ground. Other raptors including *Falco* species have been reported, if only rarely, to night-roost on the ground in a flat, sparsely timbered region of Australia known as the Channel Country, and all incidences involved treeless plains country (Hall 1974, Baker-Gabb 1985).

Grey Falcon individuals, in contrast, night-roost on the bare ground in any region and even when trees (and their nest) are within view. I propose that this is a consequence of the species' behaviour of keeping activity levels low at all times. That is, at the end of a given day an individual may roost at the very spot where it ended its activity, for example because the thermal updrafts ceased to support the soaring flight that these birds prefer (Chapter 2). Rather than undertake wing-beating flight to find a tree an individual may choose to roost for the night where it is. In summary, given the often sparsely vegetated environment where these birds live, these birds may roost on the bare ground, and this behaviour can be explained by the species' general behaviour of keeping activity levels low at all times.

Unexpected threats: on-ground night-roosting and climate change

Two unexpected threats to the Grey Falcon emerge from this study: night-roosting on the bare ground, and, potentially, climate change.

Night-roosting on the bare ground in the arid/semi-arid zones of Australia must have been relatively safe for it to evolve as a behaviour in Grey Falcons. This safety largely resulted from the absence of cursorial carnivores in that area that were large enough to kill an animal of Grey Falcon size (~300–600 g) (Chapter 5). With the relatively recent introduction of cats, foxes, dogs and dingoes that situation has changed dramatically. In consequence, the Grey Falcon is potentially threatened by these introduced carnivores, the threat from feral cats being verified and acute. The degree of these birds' exposure, their susceptibility on the ground, and their presumed lack of adaptive capacity in this regard suggests that this threat to the Grey Falcon is substantial.

The potential threat from climate change derives from extreme climatic events that characterize the environment in which these birds live (Chapter 5), and is a consequence of the species' behaviour to remain at all times in that environment. Heat waves, for example, and days of extremely high heat loads have the potential to threaten the survival of the individuals affected. These extreme climatic events are predicted to increase in frequency, severity, and duration over time. The identification of a potential threat from climate change to the Grey Falcon is an unexpected result of this study and had hitherto not been recognized. For example, the Grey Falcon was not included in the *Climate Change Adaption Plan for Australian Birds* (Garnett and Franklin 2014), presumably because the data available at that time did not reveal the Grey Falcon's seemingly precarious association with its arid environment that renders the species susceptible to the detrimental effects of climate change. This is, the species is confined to its arid hot environment and cannot be simply expected to move to other areas or environments because the species appears to be unable to deal with the higher relative humidity outside of this area. Of note, the potential threat from climate change arises from increasingly extreme climatic events rather than from long-term trends of climate change, such as rising average temperatures, and this can also be said for many other organisms around the world, including plants and animals (e.g., Emanuel 2005, Hance et al. 2007, Hoover et al. 2014).

Conservation measures

The main conservation measures proposed are, with decreasing priority: (1) the suppression of feral cats, foxes, dogs and dingoes in the arid zone, and (2) the global (and local) combat of climate change.

Conservation measures that have been employed for other threatened raptor species include captive breeding and the provision of artificial nest sites (e.g., Mauritius Kestrel *Falco punctatus* (Jones 2004), California Condor *Gymnogyps californianus* (Snyder et al. 1996)). However, these measures are inappropriate for the Grey Falcon. This is because the Grey Falcon is considered to have been rare for thousands of years with no evidence for a decline having been detected (Chapter 5). Breeding birds in captivity for population restoration should be considered a last resort ‘because of the inexorable genetic and phenotypic changes that occur in captive environments’ (Snyder et al. 1996, p. 338). The provision of artificial nests should be considered only if the availability of nest sites is ever shown to be a limiting factor (Newton 1979, Snyder et al. 1996, Jones 2004). However, for the Grey Falcon factors other than nest availability are more likely to be responsible for the small size of the species’ population, namely the restriction of the entire Grey Falcon population to a hot arid environment that is characterized by unpredictable and extreme climatic events.

6.3 Future research directions

Mortality risks and reproduction rates are key aspects of a species’ ecology (e.g., Andrewartha and Birch 1954, Walter and Hengeveld 2014). For the Grey Falcon, information on neither of these two aspects is available. Investigations into these aspects require an understanding of the specific requirements and tolerances of the species in response to the environment in which the individuals under investigation live (Walter and Hengeveld 2014). Information in regard to the individuals' tolerances is provided, for the first time, by this thesis. Their species-specific requirements are, however, still little understood.

Also, research into the questions 'what makes them leave?', 'what makes them stay?', 'what makes them breed?' is needed (i) to understand their movement patterns and what influences them most strongly, and (ii) because the answers to these questions are prerequisite to investigations of mortality and reproductive rates of Grey Falcons. An understanding of the species' (age-dependent) mortality and reproductive rates, and their causes, may help to explain the extremely small, but in the long term apparently stable, size of the population of the Grey Falcon.

6.4 Synthesis

I examined three major aspects of the ecology of the Grey Falcon. The aspects included the general levels of their day-to-day activities, the duration of the dependency period of the young, and the patterns of their movements. The behaviour of these birds showed, consistently, a markedly low level of physical exertion. Because the fields of investigation included key aspects of the ecology of these organisms, namely food acquisition, reproduction, and movement, the congruence in the findings suggests that the ecology of the Grey Falcon in general is governed by the principle of keeping physical exertion low. Keeping levels of physical exertion low helps these birds to thermoregulate during periods of high heat loads by keeping endogenous heat production low. This enables the individuals of the Grey Falcon to respond to adverse climatic events without delay because it enables them to move when it becomes necessary, i.e. regardless of weather conditions at that very moment, and even during periods of extremely high heat loads. Thus it appears that this behaviour enables the Grey Falcon's permanent residence in the hot arid and semi-arid zone of Australia. I, therefore, interpret this behaviour as an adaptation to the species' hot arid environment, one that is characterized by extreme and unpredictable climatic events.

6.5 Implications for the genus *Falco*

This study presents the Grey Falcon as the only member of its genus with the entire population being restricted to an extreme arid-hot environment. The behaviours that enable the individuals to remain in this environment are unique among *Falco*, in fact unique among diurnal raptors. Other species of *Falco* show similarly unusual behaviours that seem to enable the individuals to cope with their extreme environments. For example, individuals of the circumpolar Gyrfalcon *F. rusticolus* spend extensive periods during the arctic winter at sea far from land, 'presumably resting on icebergs and feeding on seabirds' (Burnham and Newton 2011, p. 468). Further, individuals of the desert-living Lanner Falcon *F. biarmicus* breed in hyper-arid areas of the Sahara, and nest on the bare ground in areas where trees and artificial structures (e.g., power-line pylons) are unavailable (Goodman and Haynes 1989, 1992). Autecological studies into the specific behavioural, morphological and physiological adaptations of these two falcons appear warranted.

Both of these extreme environments, i.e. the High Arctic (including Greenland) and the most arid hot parts of northern Africa, are inhabited by members of the genus *Falco* but not by any member of *Accipter* (Thiollay 1994, White et al. 1994). *Falco* and *Accipiter* each are by far the species-richest genus in their respective family, Falconidae (64 spp., thereof 38 in *Falco*) and Accipitridae (248 spp., thereof 48 in *Accipiter*) (del Hoyo and Collar 2014). Both genera seem to posses, therefore, similar evolutionary capacities for diversification. Further, both genera are represented in all 11 zoogeographic realms identified by Holt et al. (2013). The circumstance that falcons but no accipiters persist in the extreme environments mentioned above, some of the most extreme environments on earth, suggests, therefore, that the lineage *Falco* has a particularly high capacity for adaptation to extreme environments. The Grey Falcon appears as a fine example thereof.

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Appendix 1 The 38 species of the genus *Falco*, the climate zones in which they occur, their diets, and their conservation statuses (CS). Species names according to del Hoyo and Collar (2014). Occurrences according to eBird http://ebird.org/ebird/map/ (accessed 13 July 2016), except Grey Falcon (this study). Climate zones according to the Köppen-Geiger climate classification (Peel et al. 2007); 'A', tropical; 'B', Arid; 'C', Temperate; 'D', Cold; 'E', Polar. Diets according to White et al. (1994) unless indicated otherwise, except Grey Falcon (this study). For species that are threatened, rare, or restricted to one climate zone, indicated are range size (except for Mauritius Kestrel, for which the size of the distribution area was not provided *) and estimated number of mature individuals in the population. Range size, population size estimate, and conservation status taken from the species fact sheets published by BirdLife International http://www.birdlife.org/ (accessed 13 July 2016). 'LC', least concern; 'NT', near threatened; 'VU', vulnerable; 'EN', endangered. Highlight indicates Grey Falcon.

Falco sp.	Common name	Occurrence (climate zones)					Main diet	Number of mature individuals	Range size (km²)	CS
naumanni	Lesser Kestrel		B	C	D		Insects			LC
tinnunculus	Common Kestrel	A	B	C	D	E	Mammals			LC
newtoni	Madagascar Kestrel	A	B	C			Insects			LC
punctatus	Mauritius Kestrel	A					Geckos	250–300	<1 865 [1]	EN
araeus [2]	Seychelles Kestrel	A					Lizards	~530	220	VU
moluccensis	Spotted Kestrel	A					Mammals, lizards, insects, birds	10's of 1000's	465 000	LC
cenchroides	Nankeen Kestrel	A	B	C			Invertebrates, vertebrates			LC
sparverius	American Kestrel	A	B	C	D		Insects, vertebrates			LC
rupicoloides	Greater Kestrel	A	B	C			Arthropods, also birds and lizards			LC
alopex	Fox Kestrel	A	B				Insects, mammals, lizards, birds			LC
ardosiaceus	Grey Kestrel	A	B	C			Grasshoppers, reptiles			LC
dickinsoni	Dickinson's Kestrel	A	B	C			Birds, lizards			LC
zoniventris	Banded Kestrel	A	B	C			Lizards			LC
chicquera	Red-headed Falcon	A	B	C			Birds, bats			NT
ruficollis	Red-necked Falcon	A	B	C			Birds, bats			LC

[1] The species occurs only on the island of Mauritius, which has a surface area of 1865 km².
[2] Previously referred to as *F. araea* (e.g., Monroe and Sibley 1993, White et al. 1994).

[continued]

Appendix 1 (cont.)

Falco sp.	Common name	Occurrence (climate zones)	Main diet	Number of mature individuals	Range size (km²)	CS
vespertinus	Red-footed Falcon	B C D	Insects; chicks fed with vertebrates			NT
amurensis	Amur Falcon	A B C	Insects			LC
eleonorae	Eleonora's Falcon	A B C	Insects; birds when breeding			LC
concolor	Sooty Falcon	A B C	Insects; birds when breeding			NT
columbarius	Merlin	A B C D E	Various; birds when breeding			LC
rufigularis	Bat Falcon	A B C	Bats, birds, insects			LC
deiroleucus	Orange-breasted Falcon	A B C	Birds, also bats			NT
femoralis	Aplomado Falcon	A B C E	Birds and a variety of other animals			LC
subbuteo	Eurasian Hobby	A B C D	Insects, also birds when breeding			LC
cuvierii	African Hobby	A B C	Insects; birds when breeding			LC
severus	Oriental Hobby	A C	Insects, birds, bats			LC
longipennis	Australian Hobby	A B C	Birds, bats, insects			LC
novaeseelandiae	New Zealand Falcon	C	Birds, also other animals	2 500–9 999	149 000	NT
berigora	Brown Falcon	A B C	A variety of animals			LC
hypoleucos	Grey Falcon	B	Birds almost exclusively, at all ages	≤999	5 370 000	VU
subniger	Black Falcon	A B C	Mammals, birds, insects, carrion	670–6 700	5 910 000	LC
biarmicus	Lanner Falcon	A B C D	Birds, also other animals			LC
jugger	Laggar Falcon	A B C	Birds, also mammals, insects			NT
cherrug	Saker Falcon	B C D	Mammals, birds less important	12 800–30 800	7 580 000	EN
rusticolus	Gyrfalcon	C D E	Birds and mammals			LC
mexicanus	Prairie Falcon	A B C	Mammals and birds			LC
peregrinus	Peregrine Falcon	A B C D E	Birds; fledglings hunt insects [3]			LC
fasciinucha	Taita Falcon	A C	Birds, few insects	500–1 000	501 000	VU

[3] Cade (1982)

Appendix 2 List of the 38 species of the genus *Falco* (del Hoyo and Collar 2014) and their movement patterns according to White et al. (1994). Highlight indicates Grey Falcon.

Falco sp.	Common name	sedentary	migratory	dispersive	irruptive	nomadic
naumanni	Lesser Kestrel		x			winter
tinnunculus	Common Kestrel	x	x	x		
newtoni	Madagascar Kestrel	x		?		
punctatus	Mauritius Kestrel	x				
araea	Seychelles Kestrel	x		limited		
moluccensis	Spotted Kestrel	x				
cenchroides	Australian Kestrel	x	x		x	
sparverius	American Kestrel	x	x			
rupicoloides	Greater Kestrel	x				parts
alopex	Fox Kestrel	x	x			
ardosiaceus	Grey Kestrel	x				
dickinsoni	Dickinson's Kestrel	x				
zoniventris	Banded Kestrel	x				
chicquera	Red-headed Falcon	x				x
ruficollis	Red-necked Falcon	x				x
vespertinus	Red-footed Falcon		x			
amurensis	Amur Falcon		x			
eleonorae	Eleonora's Falcon		x			
concolor	Sooty Falcon		x			
columbarius	Merlin	parts	x			
rufigularis	Bat Falcon	x				
deiroleucus	Orange-breasted F.	x				
femoralis	Aplomado Falcon	parts	x			
subbuteo	Eurasian Hobby	parts	x			
cuvierii	African Hobby	x	parts?			
severus	Oriental Hobby	x	x			
longipennis	Australian Hobby	x	x			
novaeseelandiae	New Zealand Falcon	x				
berigora	Brown Falcon	x			x	
hypoleucos [1]	Grey Falcon [1]	?	parts?	?		? [1]
subniger [1]	Black Falcon [1]		?	?	?	? [1]
biarmicus	Lanner Falcon	x				x
jugger	Laggar Falcon	x				
cherrug	Saker Falcon	parts	mainly	parts		
rusticolus	Gyrfalcon	x			?	
mexicanus	Prairie Falcon	some	x	x		
peregrinus	Peregrine Falcon	x	x			
fasciinucha	Taita Falcon	x		x		
Totals	38 species of *Falco*	31 + 1 '?'	17 + 3 '?'	5 + 3 '?'	2 + 2 '?'	5 + 2 '?'

[1] Movements of Grey Falcon and Black Falcon are "poorly understood" (White et al. 1994, p. 270).

Appendix 3 Specimens of *Falco* species held at faunal collections in the USA included in this study. 'ANSP', Academy of Natural Sciences Philadelphia; 'AMNH', American Museum of Natural History, New York; 'MVZ', Museum of Vertebrate Zoology, University of California, Berkeley; 'NSW', 'NT', 'Qld', 'SA', 'TAS', and 'WA' denote states and territories of Australia; 'BC', British Columbia, Canada; 'E', 'N', 'NE', 'NW', 'SE', and 'W' denote points of the compass.

	Falco sp.	Subspecies [1]	Origin [1]	Sex [1]	Sex [2]	Accession no.
1	*hypoleucos*		W. Australia [3]	m	f	ANSP-2099
2			S. Australia [3]	f	f	ANSP-2098
3			Broken Hill NSW	-	m	AMNH-537626
4			Parry's Creek WA	m	m	AMNH-537622
5			Broken Hill NSW	m	m	AMNH-537625
6			(Coll. C. Smith)	m	m	AMNH-537623
7			(Coll. C. Smith)	f	f	AMNH-537624
8			Oodnadatta SA	m	m	AMNH-537627
9			Cooper Creek SA	m	m	MVZ-143038
10		*ashbyi*	SA	f?	m	AMNH-537628
11	*subniger*		Birdsville Qld	m	m	AMNH-343600
12			Normanton Qld	f?	m	AMNH-537097
13			Windorah Qld	m	m	AMNH-343602
14			Alexandria NT	f	f	AMNH-538762
15	*chicquera*		India	-	m	ANSP-55984
16			India	f	m	ANSP-2133
17			Sudan	f	m	ANSP-100287
18		*ruficollis*	Sudan	f	f	ANSP-118662
19			Sudan	m	f	ANSP-118663
20			Fazogloa, Africa	-	m	ANSP-2138
21	*mexicanus*		Dakota, USA	m	m	ANSP-74948
22			Dakota, USA	-	m	ANSP-74949
23			Dakota, USA	-	f	ANSP-26392
24			Utah, USA	f	f	ANSP-84499
25			New Mexico, USA	-	m	ANSP-2173
26			New Mexico, USA	-	m	ANSP-2174
27	*rusticolus*		Greenland	-	f	ANSP-2166
28			Greenland	-	f	ANSP-30140
29			Greenland	f	f	ANSP-30194
30			Greenland	-	m	ANSP-2168
31			Greenland	-	f	ANSP-2169
32			Greenland	-	f	ANSP-30142
33			N Greenland	-	f	ANSP-26967
34		*candicans*	W Greenland	f	m	AMNH-537028
35			Greenland	m	m	AMNH-352905
36			Baffin Is., Canada	-	m	AMNH-787339
37			Baffin Ld. 69º N, Canada	-	m	AMNH-525526
38		*islandicus*	N Iceland	m	m	AMNH-448961
39	*deiroleucus*		Province Napo, Ecuador	f	f	ANSP-184553
40			Brazil	m	m	ANSP-2129
41			Cayenne, French Guiana	-	m	ANSP-2130
42			La Hondura, Costa Rica	m	m	ANSP-143111

[continued]

Appendix 3 (cont.)

	Falco sp.	subspecies [1]	Origin [1]	Sex [1]	Sex [2]	Accession no.
43	*biarmicus*		Lundazi, N Rhodesia	f	f	ANSP-165996
44			Lundazi, N Rhodesia	f	f	ANSP-165997
45			Upper Egypt	m	m	AMNH-536903
46			Middle Egypt	f	f	AMNH-536900
47	*jugger*		Susa Punjab, India	f	f	AMNH-448664
48			Susa Punjab, India	m	m	AMNH-448662
49			Susa Punjab, India	f	f	AMNH-300428
50			Susa Punjab, India	f	f	AMNH-448663
51			India	-	m	AMNH-536992
52	*eleonorae*		Mogador Is., Morocco	m	m	AMNH-537590
53			Mogador Is., Morocco	m	m	AMNH-537591
54			Mogador Is., Morocco	m	m	AMNH-537593
55			Haha, Morocco	f	f	AMNH-537604
56	*concolor*		Madagascar	f	f	AMNH-410968
57			Tubor, Madagascar	m	m	AMNH-419955
18			Mogador Is., Morocco	f	f	AMNH-537594
59			Mogador Is., Morocco	f	f	AMNH-537595
60	*peregrinus*	*anatum*	Colorado, USA	m	f	ANSP-43470
61			Colorado, USA	f	f	ANSP-43471
62			Utah, USA	m	m	ANSP-84500
63			Utah, USA	f	f	ANSP-84501
64		*arabicus* [4]	Eritrea	m	m	AMNH-537343
65		*babylonicus*	(?)	-	f	AMNH-776727
66			Luxor, Egypt	m	m	AMNH-537342
67		*brookei* [5]	Russia	-	f	ANSP-55979
68			Russia	-	f	ANSP-55980
69		*calidus* [5]	Okinawa, Japan	f	f	ANSP-60713
70			Chieng, Thailand	m	m	ANSP-87528
71			Sorong, New Guinea	m	m	ANSP-140563
72		*cassini*	Patagonia	f	m	ANSP-78837
73			Columbia	m	f	ANSP-164716
74			Falkland Islands	m	m	AMNH-166289
75		*ernesti*	Vogelkop, New Guinea	f	f	ANSP-132943
76			British New Guinea	m	m	AMNH-537358
77			SE New Guinea	m	m	AMNH-537362
78			Dutch New Guinea	-	f	AMNH-537357
79			New Guinea	f	f	AMNH-537360
80		*macropus*	Tailem Bend SA	f	f	ANSP-189852
81			TAS	m	m	ANSP-2080
82			TAS	f	f	ANSP-2081
83			(? WA)	f	f	ANSP-2082
84		*minor*	Cape of Good Hope	-	m	ANSP-2065
85			Cape of Good Hope	-	m	ANSP-2066
86			Blue Nile	m	m	AMNH-537377
87			Zanzibar, Tanzania	m	m	AMNH-537379
88		*nesiotes*	Fiji Is.	-	m	AMNH-216292
89			New Hebrides Is.	-	m	AMNH-336721
90		*pealei*	Langara Is., Canada	m	m	ANSP-100981
91			Graham Is., BC	f	f	ANSP-100987
92			BC	-	m	AMNH-750454
93			BC	m	m	AMNH-750402

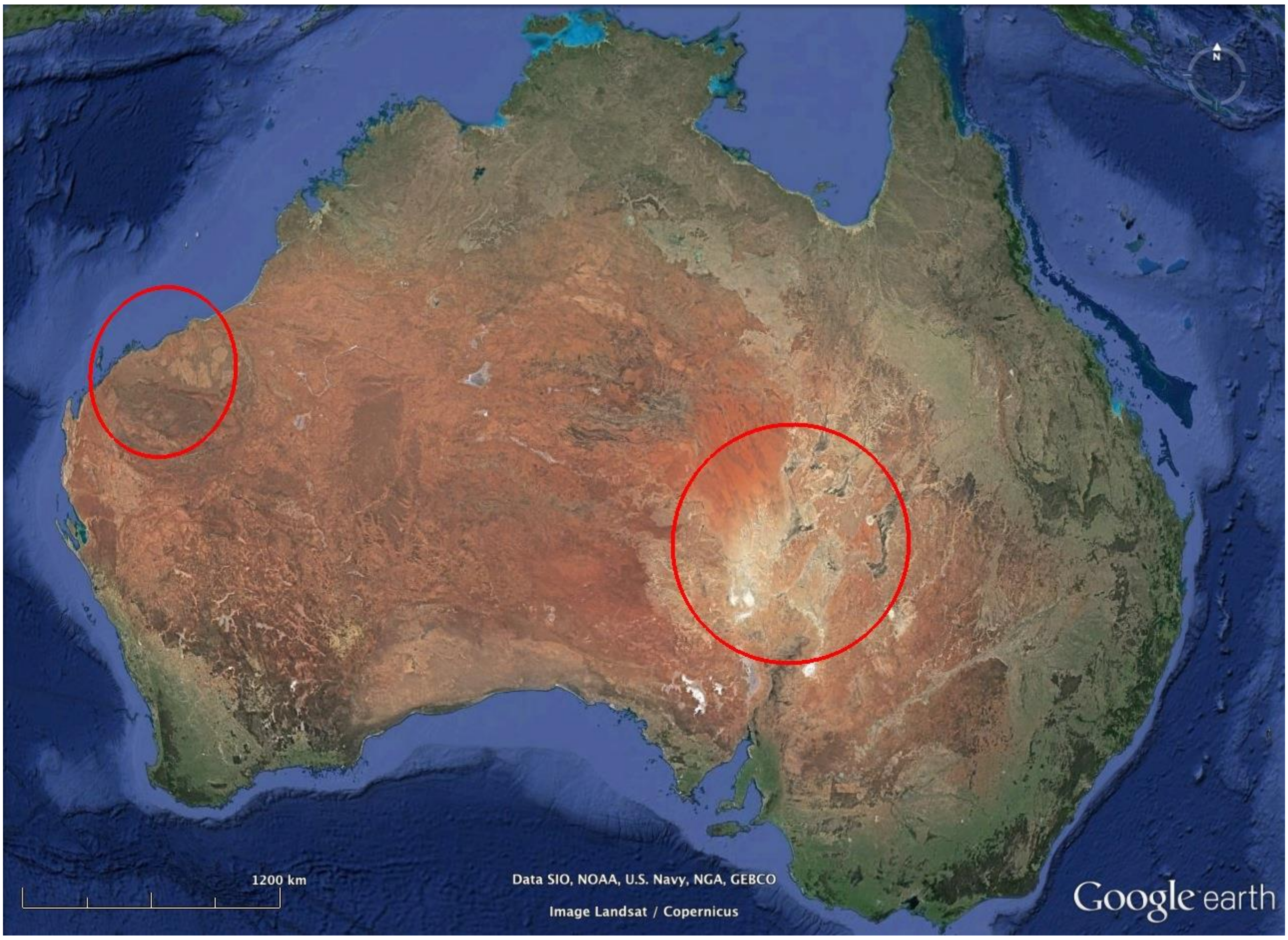
[continued]

Appendix 3 (cont.)

	Falco sp.	subspecies [1]	Origin [1]	Sex [1]	Sex [2]	Accession no.
94	*peregrinus*	*pelegrinoides*	Sudan	m	m	ANSP-100286
95	(cont.)		Canary Is.	f	f	AMNH-537298
96			Canary Is.	m	m	AMNH-537296
97			Canary Is.	-	f	AMNH-537295
98		*perconfuscus*[6]	Congo	m	m	ANSP-537380
99			Rustenburg, Transvaal	m	m	ANSP-537381
100		*peregrinator*	India	f	f	ANSP-2059
101			India	m	m	ANSP-2084
102			India	f	f	ANSP-2085
103			Foochow, China	-	f	AMNH-537351
104			Foochow, China	m	m	AMNH-537350
105		*peregrinus*	N Wales, Great Britain	m	m	AMNH-537159
106			NW Scotland	m	m	AMNH-357152
107			Wales, Great Britain	-	f	AMNH-750428
108			Pommern (NE Germany)	-	f	AMNH-537174
109		*radama*	Madagascar	f	f	AMNH-410954
110			Central Madagascar	m	m	AMNH-196639
111			E Madagascar	m	m	AMNH-537382
112		*tundrius*	NW Territory, Canada	m	m	AMNH-119372
113			Chamisso Is., Alaska	m	m	AMNH-750435
114			Hudson Bay, Canada	f	f	AMNH-442650
115			Kakuk, Greenland	m	m	AMNH-750434

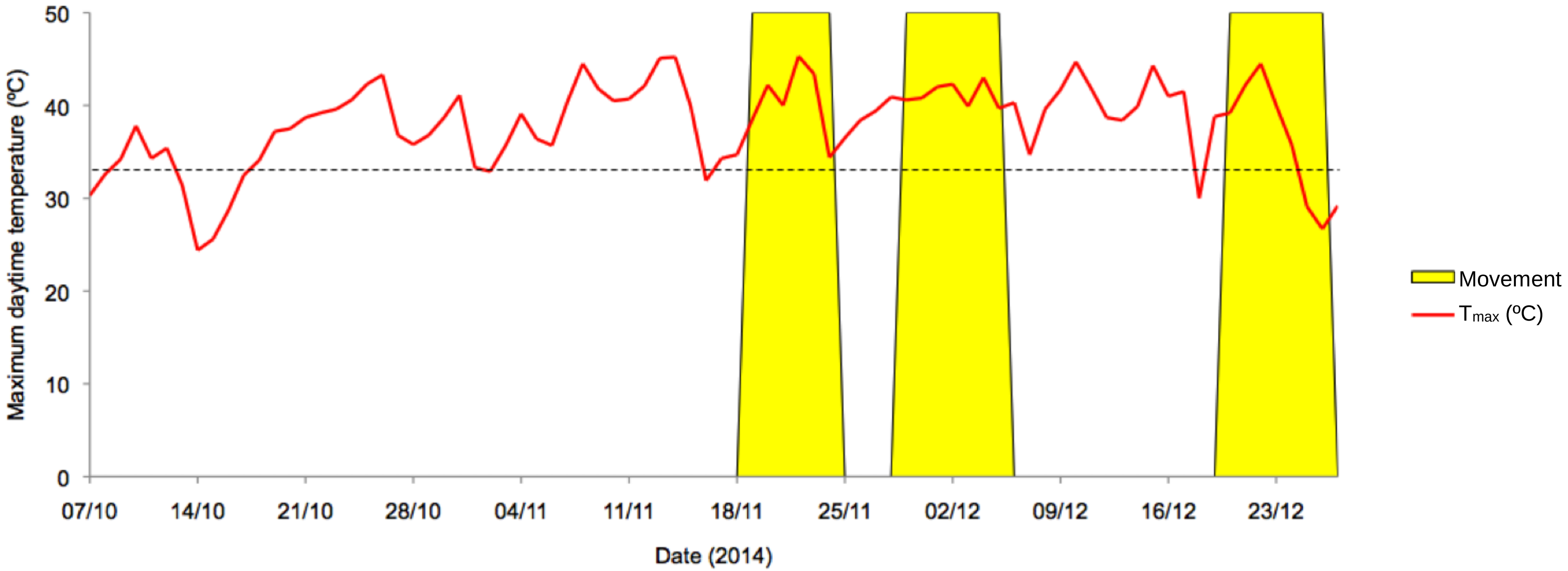
[1] According to the information provided on the label.
[2] Reassessed by measurement, see text.
[3] Almost certainly erroneous, presumable Deport Glen, NW NSW; see Schoenjahn (2010a).
[4] *F. peregrinus arabicus* is now commonly included in *F. p. pelegrinoides* (White et al. 2013).
[5] Excluded from the analyses of this study; see text.
[6] *F. peregrinus perconfuscus* is now commonly included in *F. p. minor* (White et al. 2013).

Appendix 4 Spatial distribution of breeding events recorded for 2015 (n = 6) (see text). Two breeding events were in western Australia, and four in the central and easterly parts of inland Australia (Table 3.6). Precise locations withheld.



Appendix 5 Maximum daytime temperature during the period during which three individual Grey Falcons were satellite-tracked (birds number 3, 4, and 6 in Table 4.1, and represented in plots, below, labelled A), B) and C) respectively. Note that C) is broken down further into time periods labelled C1) to C4)). The temperature records were obtained from the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/data). The yellow columns indicate periods of wide-ranging trips, i.e. trips outside the quasi-sedentary area that the bird used at that time (see text). The dashed line indicates 33ºC, the temperature that was suggested to reflect the turning point in the thermoregulatory behaviour of these birds from heat-seeking to heat-avoiding (Chapter 2). Dates are shown in dd/mm or dd/mm/yy. A broken temperature line indicates unavailable data.

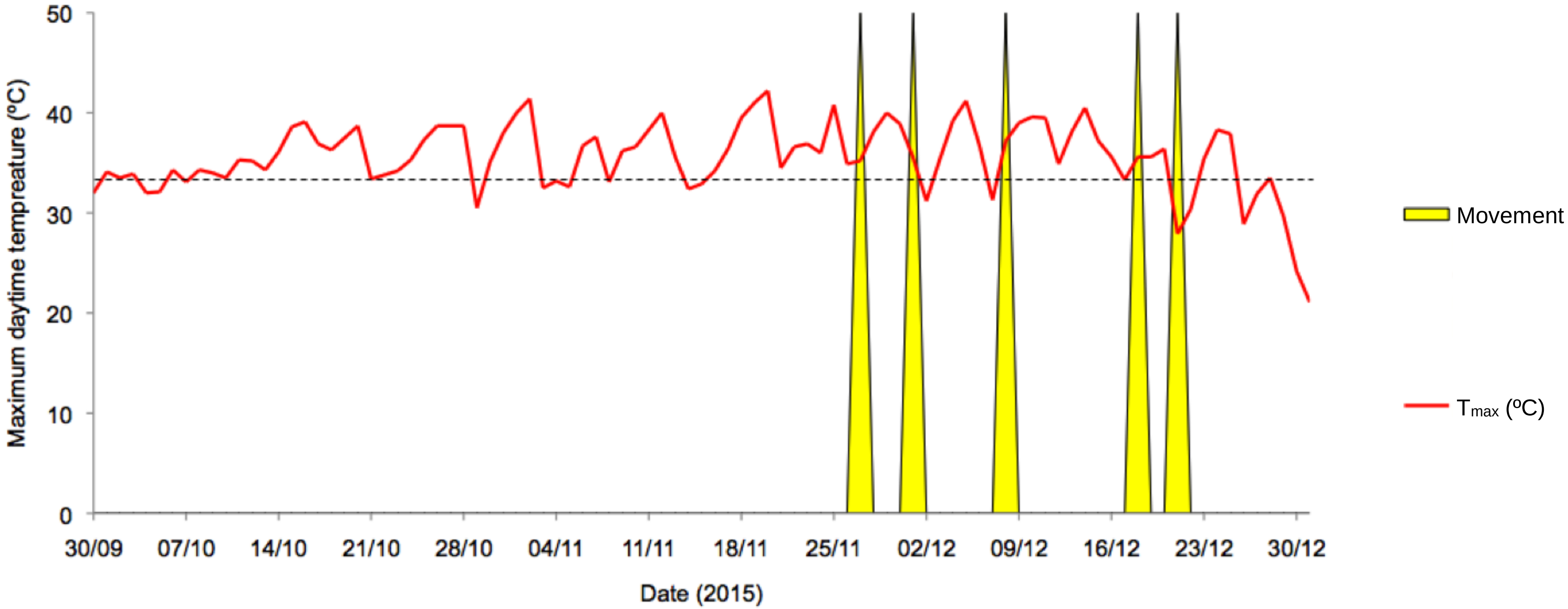
A) Adult male Argos ID 141276 (Qld), tracked from 7 Oct. 2014 to 27 Dec. 2014. The temperatures pertain to Birdsville Airport. When tagged, the bird was breeding with three young in the nest.



[continued]

Appendix 5 (cont.)

B) Adult male Argos ID 141276 (NT), satellite-tracked from 30 Sep. 2015 to 31 Dec. 2015. The temperatures pertain to Alice Springs Airport. When tagged, the bird was not breeding but closely associated with its female partner and a yearling female.

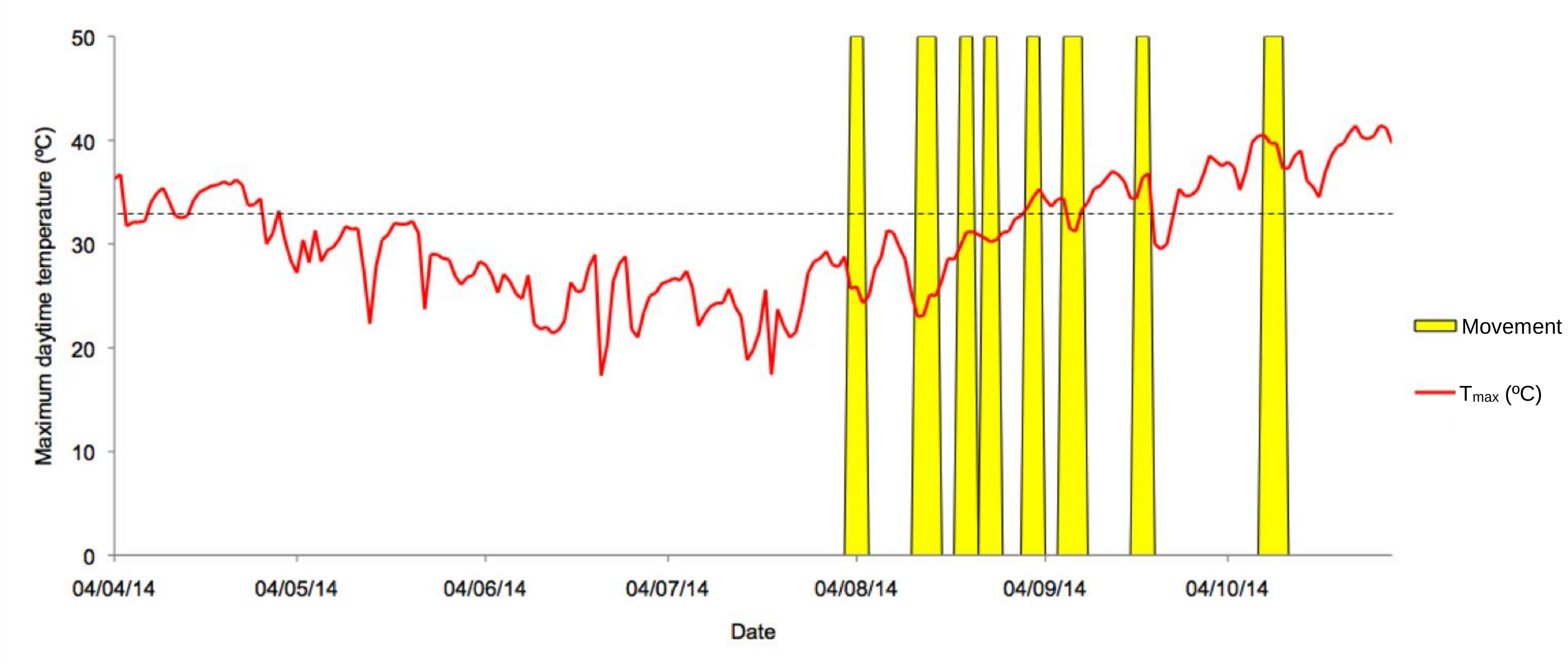


[continued]

Appendix 5 (cont.)

C) Female Argos ID 134881, satellite-tracked from 4 Apr. 2014 to 8 June 2016. The temperatures pertain to Wittenoom because these temperatures matched better with the temperatures recorded by me (Chapter 2) than the temperature for Learmont, which is located closer to the relevant area but situated on a peninsula and thus experiences a more maritime climate.

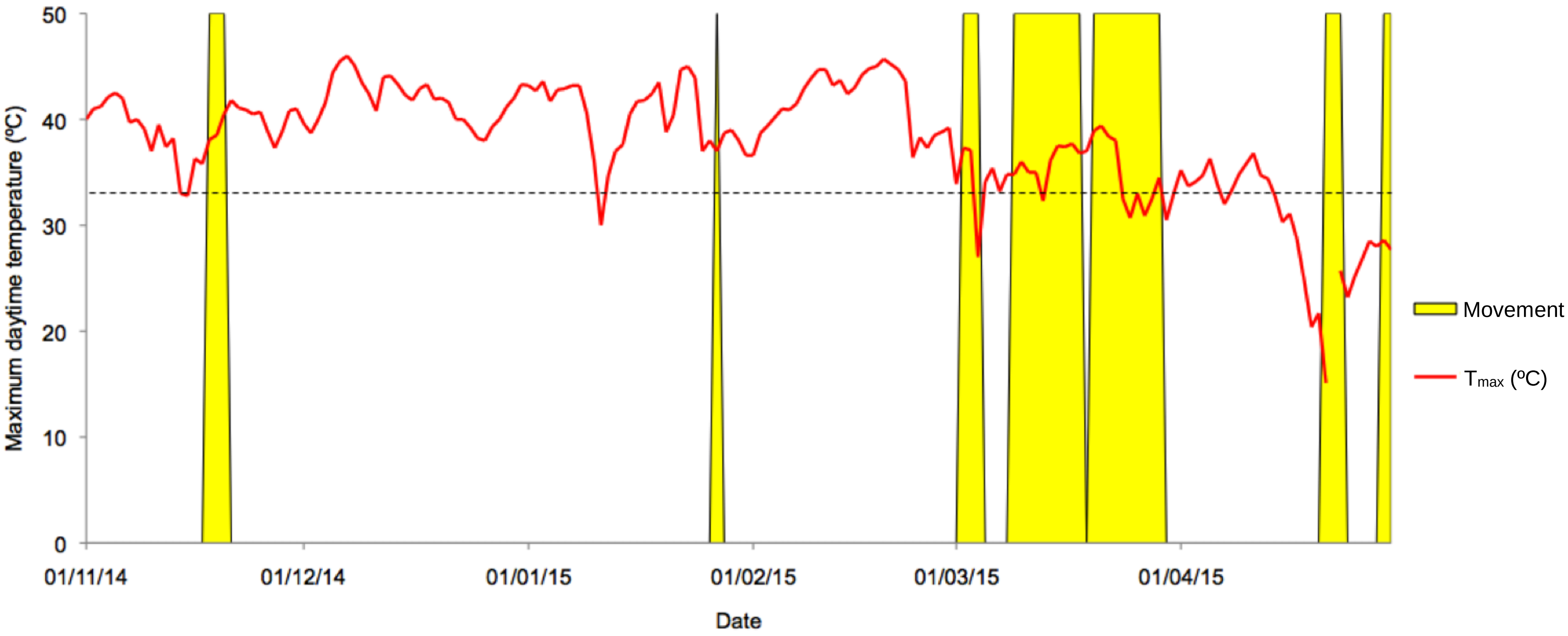
C1) Period 4 Apr. 2014 to 31 Oct. 2014 (bird Argos ID 134881).



[continued]

Appendix 5 (cont.)

C2) Period 1 Nov. 2014 to 30 Apr. 2015 (bird Argos ID 134881).



[continued]

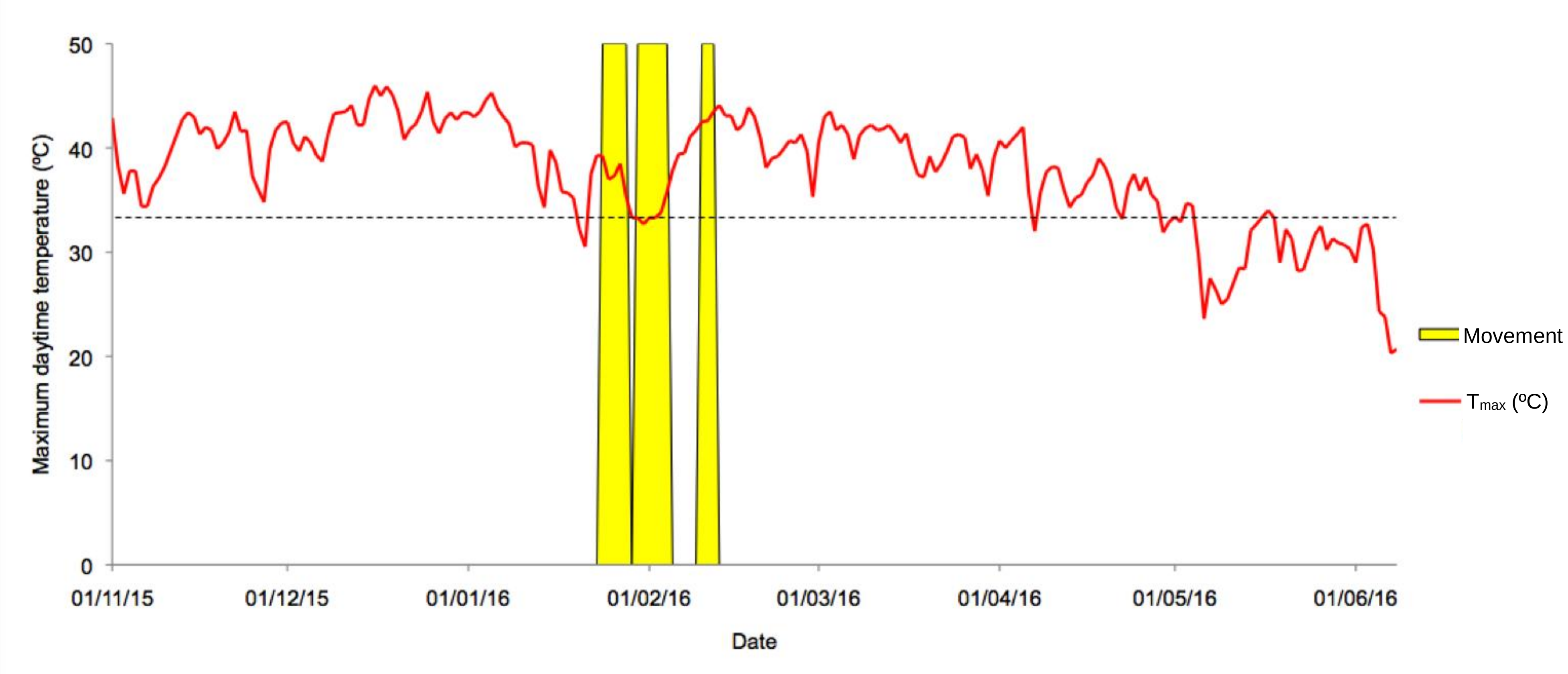
Appendix 5 (cont.)

C3) Period 1 May 2015 to 31 Oct. 2015 (bird Argos ID 134881). The bout of wide-ranging movements between 22 June and 23 July 2016 led to the bird's shift from one quasi-sedentary area to the next.

[continued]

Appendix 5 (cont.)

C4) Period 1 Nov. 2015 to 8 June 2016 (bird Argos ID 134881). The bout of wide-ranging movements between 25 Jan. and 4 Feb. 2016 led to the bird's shift from one quasi-sedentary area to the next.



Appendix 6 Animal Ethics Committee approval certificates.

A) Animal Care and Ethics Committee of the NSW Department of Primary Industries. Period 22 Mar. 2013 to 22 Mar. 2016.

TRIM File 10/1354
DG ACEC Meeting 153, 18 March 2013

ANIMAL CARE AND ETHICS COMMITTEE OF THE DIRECTOR-GENERAL OF DEPARTMENT OF PRIMARY INDUSTRIES

CERTIFICATE OF APPROVAL

Mr Jonny Schoenjahn
1 Elimatta Way
CITY BEACH WA 6015

Is approved to conduct the following research

MOVEMENTS AND GENETICS OF GREY FALCONS

as approved by and in accordance with the

ANIMAL CARE AND ETHICS COMMITTEE OF THE DIRECTOR-GENERAL OF DEPARTMENT OF PRIMARY INDUSTRIES

being animal research carried out in accordance with the Code of Practice, for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence

This approval remains in force from **22 March 2013** to **22 March 2016** unless suspended, cancelled or surrendered

Amanda Paul

AMANDA PAUL
EXECUTIVE OFFICER (DG ACEC)
ANIMAL WELFARE UNIT

Date: 4 April 2013

NSW Department of Primary Industries, an office of the Department of Trade and Investment, Regional Infrastructure and Services

Delegate of the Director-General of the Department of Trade and Investment, Regional Infrastructure and Services

[continued]

Appendix 6 (cont.)

B) Animal Care and Ethics Committee of the NSW Department of Primary Industries. Period 22 Mar. 2016 to 22 Mar. 2019.

TRIM 16/350 Secretary's ACEC 174 21 MARCH 2016

ANIMAL CARE AND ETHICS COMMITTEE OF

THE SECRETARY
NSW INDUSTRY, SKILLS AND REGIONAL DEVELOPMENT

CERTIFICATE OF APPROVAL

Mr Jonny Schoenjahn
1 Elimatta Way
CITY BEACH WA 6015

Is approved to conduct the following research

MOVEMENTS AND GENETICS OF GREY FALCONS

as approved by and in accordance with the

ANIMAL CARE AND ETHICS COMMITTEE OF THE SECRETARY NSW INDUSTRY, SKILLS AND REGIONAL DEVELOPMENT

Being animal research carried out in accordance with the Code of Practice, for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence

This approval remains in force from **22 March 2016** to **22 March 2019** unless suspended, cancelled or surrendered

Amanda Paul

AMANDA PAUL
EXECUTIVE OFFICER (Secretary's ACEC)*
ANIMAL WELFARE UNIT

29 March 2016

NSW Department of Primary Industries, an office of NSW Department of Industry, Skills & Regional Development

*Delegate of the Secretary of the Department of Industry, Skills & Regional Development

[continued]

Appendix 6 (cont.)

C) Animal Ethics Committee of Charles Darwin University, NT.

Period 16 Apr. 2014 to 16 Apr. 2016.

CHARLES DARWIN UNIVERSITY

CHARLES DARWIN UNIVERSITY
Ellengowan Drive, Darwin, Northern Territory 0909
ABN 54093 513 649 | CRICOS Provider No. 00300K | RTO Provider No. 0373
cdu.edu.au

02nd May 2014

Mr Jonny Schoenjahn
1 Elimatta Way
City Beach WA 6015
Dear Mr Schoenjahn

Re: A 12018 Movements and genetics of grey falcons
Animal Ethics Committee Project Renewal Approval

The Charles Darwin University Animal Ethics Committee considered and approved the abovementioned project at meeting 3/12, held on 16th April 2014.

Ethics approval is granted for a maximum period of two years and expires on 16/4/2016.

Approvals are provided for teaching and research projects on the following conditions:

- In undertaking their projects, researchers and teachers must observe the requirements of the *NT Animal Welfare* Act and the *Australian Code of Practice for the Care and Use of Animals for Scientific Purposes;*
- The decisions and any specific conditions imposed by the Animal Ethics Committee, in approving
- this project, must be observed at all times, with any adverse events being notified to the AEC immediately.
- Variations to staffing and/or methodology must be approved by the Animal Ethics Committee in advance of the variations taking place or staff commencing work on the project.
- Investigators must make their research project documentation and the facilities within which projects may be conducted available to the Animal Ethics Committee for inspection upon request.
- Investigators must submit a progress report to the AEC one year following the approval date.
- Projects extending beyond the period of approval will need to be renewed via submission of a new project application.
- Upon completion of your project, you are required to submit a final report to the Committee.

All necessary forms are available on the CDU web site at:

http://www.cdu.edu.au/research/office/appaec.html.

If you have any queries regarding your conditions of approval, please direct them in the first instance to the Ethics Administration Officer, who is based in the CDU Office of Research and Innovation.

Our best wishes for the success of your project.

Yours sincerely

Professor Keith Christian
Chair
CDU Animal Ethics Committee

OFFICE OF RESEARCH AND INNOVATION, ETHICS
T. +61 8 8946 6923| F. +61 8 8946 7066 | E. cdu-ethics@cdu.edu.au
Casuarina Campus

CHANGE YOUR WORLD

[continued]

Appendix 6 (cont.)

D) Animal Ethics Committee of Charles Darwin University, NT.

Period 30 Mar. 2016 to 30 Mar. 2020.

CHARLES DARWIN UNIVERSITY

ANIMAL ETHICS COMMITTEE
Certificate of Project Approval

This is to certify that the animal research project:

A12018
Movements and genetics of grey falcons
Jonny Schoenjahn-29 19/07/2014

has been granted approval by the CDU AEC for the period:

30/03/2016 to 30/03/2020

Using no more per annum than:

Grey Falcon *(Falco hypoleucos)* **10**

Animal Research Permits

The AEC has issued the following Animal Research Permits under Section 48 of the *Animal Welfare Act* to the following investigators:

Principal Investigator

Mr Jonny Schoenjahn

Animal Research permits remain in force for two years after the date of approval. If the project continues after this date, permit renewal applications (i.e. Form A and B Declarations) must be submitted.

Special Conditions of Project Approval

Location: Northern Territory and Western Australian all areas

AEC Inspections

Inspections of research projects are obligatory. However due to the nature of your project, the AEC may be unable to carry out a physical inspection as required by the Code. Therefore, in place of a physical inspection, the AEC requires you to provide the following information with the submission of each of your annual **Progress Reports: video or photographic material showing project procedures, clinical records, animal handling, and if applicable animal housing.**

Keith Christian

Signature
Issued by Professor Keith Christian,
Chair of the CDU Animal Ethics Committee
on behalf of the Charles Darwin University

[continued]

Appendix 6 (cont.)

E1) NEWMA Animal Ethics Committee of The University of Queensland.

Period 15 Sep. 2014 to 15 Sep. 2017. Page 1 of 2.

THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

UQ Research and Innovation
Director, Research Management Office
Nicole Thompson

Animal Ethics Approval Certificate

12-Sep-2014

Please check all details below and inform the Animal Welfare Unit within 10 working days if anything is incorrect.

Activity Details

Chief Investigator:	Dr David Booth
Title:	Movements and Genetics of Grey Falcons
AEC Approval Number:	SBS/308/14
Previous AEC Number:	
Approval Duration:	15-Sep-2014 to 15-Sep-2017
Funding Body:	
Group:	Native and exotic wildlife and marine animals
Other Staff/Students:	Gimme Walter, Jonny Schoenjahn
Location(s):	Other New South Wales Location Other Northern Territory Location Other Queensland Location Other South Australian Location Other Tasmanian Location Other Victorian Location Other Western Australian Location

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Native Wild Birds		Other	Mix	Natural Habitat	0	0

Permits

Provisos

Animal numbers are not shown on this approval certificate, as the approved animal numbers are provided under the below AEC Approvals.
· Department of Agriculture, Fisheries and Forestry, AEC, No. CA 2013/04/684, expiry 30/06/16
· Animal Care and Ethics Committee of the Director-General of Department of Primary Industries, No. 10/1354, expiry 22/03/16
· Charles Darwin University, AEC approval No. A 12018, expiry 16/04/16
· Wildlife Ethics Committee Approval of a Project involving Animals, No. 14/2013, expiry 30/06/2013
· Licence to take fauna for scientific purposes, Reg. 17, No. SF009923, expiry 30/06/15
This certificate is to show that the project has been ratified by a University of Queensland AEC.

Approval Details

Description	Amount	Balance
Native Wild Birds (Mix, Other, Natural Habitat)		
9 Sep 2014 Ratification	0	0

Animal Welfare Unit
UQ Research and Innovation
The University of Queensland

Cumbrae-Stewart Building
Research Road
Brisbane Qld 4072 Australia

+61 7 336 52925 (Enquiries)
+61 7 334 68710 (Enquiries)
+61 7 336 52713 (Coordinator)

animalwelfare@research.uq.edu.au
uq.edu.au/research

Page 1 of 2

[continued]

Appendix 6 (cont.)

E2) NEWMA Animal Ethics Committee of The University of Queensland.

Period 15 Sep. 2014 to 15 Sep. 2017. Page 2 of 2.

Please note the animal numbers supplied on this certificate are the total allocated for the approval duration

Please use this Approval Number:

1. When ordering animals from Animal Breeding Houses
2. For labelling of all animal cages or holding areas. In addition please include on the label, Chief Investigator's name and contact phone number.
3. When you need to communicate with this office about the project.

It is a condition of this approval that all project animal details be made available to Animal House OIC.
(UAEC Ruling 14/12/2001)

The Chief Investigator takes responsibility for ensuring all legislative, regulatory and compliance objectives are satisfied for this project.

This certificate supercedes all preceeding certificates for this project (i.e. those certificates dated before 12-Sep-2014)

Animal Welfare Unit
UQ Research and Innovation
The University of Queensland

Cumbrae-Stewart Building
Research Road
Brisbane Qld 4072 Australia

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+61 7 336 52713 (Coordinator)

animalwelfare@research.uq.edu.au
uq.edu.au/research

[continued]

Appendix 6 (cont.)

F1) Animal Ethics Committee of the Qld Department of Agriculture, Fisheries and Forestry.

	DAFF Animal Ethics	Form: AE 07
	DECISION of the ANIMAL ETHICS COMMITTEE (AEC)	

1. Applicant details

Name: Jonny Schoenjahn		
Organisation:	Centre:	
Postal Address: 1 Elimatta Way City Beach WA 6015		
Phone: 08 9385 9939	Fax: 08 9385 9801	E-Mail: jonnybird@bigpond.com

2. Project Details

Title of the Project	AEC Proposal Reference Number
Movements and Genetics of Grey Falcons.	**CA 2013/04/684**

3. AEC Decision

The project proposal has been considered by the AEC and is:

Approved as submitted

Any inquiry regarding this response should be directed to the AEC Coordinator in the first instance. The Coordinator may be contacted via the DAFF Call Centre on 13 25 23.

* Comments:

Please note that the AEC appreciated your efforts in providing such a detailed proposal.

Period of approval inclusive of the following start and end dates:	Animal type and number approved:
Approved Start Date: 1 July 2013 Approved End Date: 30 June 2016	Grey Falcon, Native wild birds - 150

Page Break

Page 1 of 1 Revised: March 2013

Period 1 July 2013 to 30 June 2016. Page 1 of 2.

[continued]

Appendix 6 (cont.)

F2) Animal Ethics Committee of the Qld Department of Agriculture, Fisheries and Forestry.

Important information

1. **This approval** is for that work as approved in this decision and only within the start and end dates unless amended by a subsequent AEC decision made in accordance with the requirements of the *Animal Care and Protection Act 2001*, the *Australian code of practice for the care and use of animals for scientific purposes* (refer to 2 b) below).

   Any animal use outside this approval will constitute a breach of Section 91 of the *Animal Care and Protection Act 2001* and is subject to a maximum penalty of 300 penalty units or one year's imprisonment.

   Unless otherwise stated, this approval applies only to work conducted within Queensland.

2. **The AEC requires the Applicant to:**

   a) ensure compliance by all investigators with all conditions set out in this decision in addition to the general requirements of the *Animal Care and Protection Act 2001*, the *Australian code of practice for the care and use of animals for scientific purposes* and all other relevant Commonwealth and State legislation.

   b) submit an Amendment Request (Form AE 08) for any proposed change to a project approval prior to that change being implemented (refer to Procedural Guideline 04);

   c) report any unexpected or adverse event that impacts on the welfare of any animal used in this project (refer to Procedural Guideline 03);

   d) submit Annual Progress Reports (Form AE 10) during February of each year; and

   e) submit a Project Completion Advice (Form AE 09) upon completion of this project.

3. **Endorsement:** Approval of your project proposal/amendment request by the AEC is not an endorsement of the project by either the Department of Agriculture, Fisheries and Forestry or the Queensland Government and is not an endorsement of the Applicant, its products or its processes generally by the AEC, Department of Agriculture, Fisheries and Forestry or the Queensland Government and no one should assert any such endorsement.

4. **Correspondence:** All correspondence with the AEC in relation to this project should be via email to your AEC contact and cite the name of the Applicant, title of the project and the AEC Proposal Reference Number.

5. **Grievance:** If the Applicant feels that the AEC has erred in its decision regarding any aspect of the project, the Applicant can instigate a grievance procedure (refer to Procedural Guideline 02).

Name of AEC	Community Access AEC
Name of AEC Chair	Lex Turner
Signature	
Date of Decision	29 April 2013

Page 2 of 2 Revised: March 2013

Period 1 July 2013 to 30 June 2016. Page 2 of 2.

[continued]

Appendix 6 (cont.)

G1) Animal Ethics Committee of the Qld Department of Agriculture and Fisheries. Period 1 July 2016 to 7 Apr. 2019. Page 1 of 2.

Queensland Government	***DAF Animal Ethics***	Form: AE 07
	DECISION of the ANIMAL ETHICS COMMITTEE (AEC)	

1. Applicant details

Name: Jonny Schoenjahn		
Organisation:		Centre:
Postal Address: 1 Elimatta Way City Beach WA 6015		
Phone: 08 9385 9939	Mobile:	E-Mail: jonnybird@bigpond.com

2. Project Details

Title of the Project	AEC Application Reference Number
Movements and Genetics of Grey Falcons.	**CA 2016/04/955**

3. AEC Decision

The project application has been considered by the AEC and is:

Approved

Any inquiry regarding this response should be directed to the AEC Coordinator or Chair in the first instance. The Coordinator of Chair may be contacted via the DAF Call Centre on 13 25 23.

Comments:

Please note the approved end date has been matched with your registration end date.

Please provide a link for feather collection and handling guidelines you will be following.

Period of approval inclusive of the following start and end dates: Approved Start Date: 1 July 2016 Approved End Date: 07 April 2019	Animal type and number approved: Grey Falcon & Native wild birds – 150

Page Break

Page 1 of 2 Revised: Sept 2015

[continued]

Appendix 6 (cont.)

G2) Animal Ethics Committee of the Qld Department of Agriculture and Fisheries. Period 1 July 2016 to 7 Apr. 2019. Page 2 of 2.

Please note the animal numbers supplied on this certificate are the total allocated for the approval duration

Please use this Approval Number:

1. When ordering animals from Animal Breeding Houses
2. For labelling of all animal cages or holding areas. In addition please include on the label, Chief Investigator's name and contact phone number.
3. When you need to communicate with this office about the project.

It is a condition of this approval that all project animal details be made available to Animal House OIC.
(UAEC Ruling 14/12/2001)

The Chief Investigator takes responsibility for ensuring all legislative, regulatory and compliance objectives are satisfied for this project.

This certificate supercedes all preceeding certificates for this project (i.e. those certificates dated before 12-Sep-2014)

Animal Welfare Unit
UQ Research and Innovation
The University of Queensland

Cumbrae-Stewart Building
Research Road
Brisbane Qld 4072 Australia

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+61 7 336 52713 (Coordinator)

animalwelfare@research.uq.edu.au
uq.edu.au/research

[continued]

Appendix 6 (cont.)

H) Wildlife Ethics Committee of the SA Department of Environment, Water and Natural Resources. Period 1 July 2013 to 30 June. 2016.

Government of South Australia
Department of Environment, Water and Natural Resources

WILDLIFE ETHICS COMMITTEE

APPROVAL OF A PROJECT INVOLVING ANIMALS

APPLICATION NUMBER: 14/2013

TITLE OF PROJECT: Movements and Genetics of Grey Falcons

APPLICANT: Mr Jonny Schoenjahn
ADDRESS: 1 Elimatta Way
City Beach WA 6015

ADDITIONAL APPROVED PERSONNEL:
NIL

APPROVAL PERIOD
From 01/07/2013 To 30/06/2016

Statistical information on numbers of animals used must be submitted at the end of each calendar year along with a final report or as soon as practicable.
Contact the Executive Officer for Report/Statistics forms.

CONDITIONS
Any adverse events including unplanned deaths must be reported immediately by phone or e-mail to the Executive officer of the Wildlife Ethics Committee. Whenever possible, an autopsy should be conducted if the cause of death is unknown.

ANIMALS APPROVED: (Scientific, Common name, procedure and number of animals).

Falco hypoleucos – Grey Falcon As captured in traps or nests: band, measure, feather sample and attach satellite transmitter if suitable and release.

2

THESE ARE THE PROCEDURES THAT HAVE BEEN APPROVED:
Traps approved
Bal-Chatri cage-traps in combination with mounted (dead) bird specimens and mist nets will be used for this project. Mist nets must be attended at all times.

- **No live lure birds are to be used under this approval.**

Procedures
When birds are captured they will be removed from the trap and blindfolded with a falconer's hood and/or placed into a PVC pipe of suitable diameter and length to stop it from struggling. The falcon will then be taken to the makeshift 'banding station' with table and chair in the shade under an awning at the side of the vehicle.

- Measurements, body weight, banding, and feather samples will be taken. If the bird is suitable age and a healthy individual it will be fitted with a harness backpack satellite transmitter.
- Birds are to be released after 60 minutes at the location of capture.

Birds will be monitored for up to 2 days after release (observation by binoculars).

Hand capture of nestlings
Nestlings will be captured by hand whilst in the nest. Birds will be placed in a holding bag. Birds will be processed; body measurements, weight, determine sex and band-size; attach colour-bands; take feather samples; return all nestlings back to the nest within 60 minutes.

- **No juveniles or nestlings are to be fitted with transmitters, backpacks or harnesses during this project**

Satellite Tracking
The movements of satellite-tagged birds are monitored by means of the satellite system operated by Argos Inc.

THESE ARE THE LOCATIONS THAT HAVE BEEN APPROVED:
State wide – South Australia

IF ANY ANIMAL IS TO BE EUTHANASED AS PART OF THIS STUDY THIS IS THE PROCEDURE THAT HAS BEEN APPROVED:
Euthanasia by cervical dislocation will be carried out by the applicant in an emergency.

SIGNED: Lynnette Kajar DATE: 16/04/2013

Lynnette Kajar
Executive Officer - Wildlife Ethics Committee
Science Resource Centre
Department of Environment, Water and Natural Resources
GPO BOX 1047, ADELAIDE SA 5001
Telephone (08) 8222 9435 Fax (08) 8124 4861
Email: DEWNR.WildlifeEthicsCommittee@sa.gov.au

[continued]

Appendix 6 (cont.)

I1) Wildlife Ethics Committee of the SA Department of Environment, Water and Natural Resources. Period 26 May 2016 to 26 May 2019. Page 1 of 3.

ZOOS SOUTH AUSTRALIA zoossa.com.au — South Australian Museum — Government of South Australia, Department of Environment, Water and Natural Resources

WILDLIFE ETHICS COMMITTEE

Approval to use animals For the Purpose of Research, Teaching or Experimentation involving animals

This Approval authorises Jonny Schoenjahn to use animals for the purposes of research in project number 13*/2016 Movements and genetics of Grey Falcons,* pursuant to Part 4 of the *Animal Welfare Act 1985* (the Act). This Approval is valid from 26/05/2016 through to 26/05/2019.

General conditions

1. The applicant must provide the Wildlife Ethics Committee with such information in relation to research involving animals as the Wildlife Ethics Committee may request pursuant to section 19(1) (d) of the Act.

2. The applicant must answer such questions in relation to teaching, research or experimentation involving animals as may be put by the Wildlife Ethics Committee pursuant to section 19(1)(e) of the Act.

3. A report on any unexpected adverse events or deaths which may occur whilst undertaking the project. Such events should be advised by email or phone to the Executive Officer of the Wildlife Ethics Committee immediately and, if an animal has died, a necropsy performed to determine the cause of death.

4. The applicant must provide to the Wildlife Ethics Committee, as soon as reasonably practical, such information as requested by the committee, including, but not limited to;

   a. Statistical information on numbers of animals used each calendar year (this includes all animals trapped and released).
   b. A final report at the conclusion of the research project.

5. Appropriate care, housing and handling of animals must be maintained at all times.

6. Appropriate post-procedural care, including required veterinary treatment must be provided for animals at all times.

7. Animals must be treated humanely and in accordance with the *Act* and *Animal Welfare Regulations 2012.*

8. The acquisition, use (including all procedures) and care of animals for the research is, pursuant to s19(2)(f) of the Act, subject to compliance with Parts 1 - 6 of the *Australian code for the care and use of animals for scientific purposes, 8th Edition 2013.* National Health and Medical Research Council Australian Research Council.

9. This approval is limited to those procedures, animal species, number of animals and locations as described in project number 13*/2016 Movements and genetics of Grey Falcons*

[continued]

Appendix 6 (cont.)

I2) Wildlife Ethics Committee of the SA Department of Environment, Water and Natural Resources. Period 26 May 2016 to 26 May 2019. Page 2 of 3.

Special Conditions

- The following personnel may participate in the research project:
  Jonny Schoenjahn
- The following animals may be used in this research project:
  Grey Falcons - *Falco hypoleucos* adult and nestlings as captured. Other non-target species of birds may be caught and will be released immediately.
- The following procedures may be undertaken in the research:
  Capture, weigh, body measurements, leg diameter, attach two bands as per ABBBS Guidelines, feather sample and if applicable attach satellite transmitter. Release after a maximum of 60 minutes at location of capture. Monitor bird for up to 2 days.

Capture methods

Bal-Chatri:, Dho-Gaza, Flap door trap, Noose carpet traps baited with mounted (dead) lure bird or fresh kill from a Grey Falcon may be used to lure Grey Falcons.
A Mist-net may also be used. All traps and mist nets must be constantly monitored at all times.
No trapping is to take place where temperatures are forecast to be 35 degrees or greater or during extreme weather conditions such as heavy rain, flooding, thunder storms, strong winds, or extreme cold.

Handling of birds

The Falcon will be blindfolded with a falconer's hood and/or placed into a PVC pipe of suitable diameter and length to stop it from struggling. Then taken to the makeshift 'banding station' with table and chair in the shade under an awning at the side of the vehicle.

Nestlings

Nestlings may only be captured when the nestlings are old enough to be left alone by the adults for 2 to 3 hours at a time.
Hand-capture all the nestlings in the nest of tree.
Researcher will climb tree with tree climbing equipment, comprising of rope, harness, rope-brakes, helmet, safety-shackles etc.
One nestling after the other will be captured and placed in separate cotton bird holding bags and placed in a cotton rucksack for the descent from the tree. At the base of the tree the bags with birds will be removed from the ruck sack and taken immediately to the canvas shade sail attached to the side of the vehicle to be processed.
One bird at a time will be processed. After processing all the nestlings will be returned to the nest within 60 minutes of first capture.

Transmitters

Argos transmitters will be fitted to the back of the bird by means of a harness.
The harness consists of two loops of Teflon ribbon. The ribbon actually is a flattened tube, flattened width 1/4 inch. The loops are threaded through the loopholes on the transmitter. The loops are made to an approximate size and can easily be pulled over the bird. The only connection that needs to be made is stitching the ends of the two loops together with cotton thread. This cotton stitching is the weak link.

[continued]

Appendix 6 (cont.)

I3) Wildlife Ethics Committee of the SA Department of Environment, Water and Natural Resources. Period 26 May 2016 to 26 May 2019. Page 3 of 3.

Biological Samples

Feather samples.

Three fully-grown feathers will be taken by tweezers from three separate locations on the breast.

Adverse events

Any unexpected adverse events or deaths which occur during this research, must be reported immediately within 24 hours of the incident occurring via email or phone message the Executive Officer of the Wildlife Ethics Committee.

Voucher specimens

Any animals that die or need to be euthanised as a direct result of this research will be prepared as museum vouchers and lodged with the South Australian Museum.

- The research project may be conducted at the following locations:
  South Australia.

- If an animal is euthanised during the research project the following procedure will be carried out:
  Cervical dislocation.

Signed:...

Lynnette Kajar
EXECUTIVE OFFICER
On behalf of the Wildlife Ethics Committee

Date of approval: 02/06/2016

Department of Environment, Water and Natural Resources
Telephone (08) 8463 6851
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