UNIVERSITY OF LIVERPOOL

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THE EVOLUTIONARY ECOLOGY OF COMPLEX SIGNALLING SYSTEMS IN UNGULATES

Diversity and flexibility in a changing world

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ABSTRACT

Understanding the ultimate and proximate causes of signal diversity, complexity, and flexibility is a key issue in the study of animal communication. In this thesis, I investigated the factors affecting inter- and intraspecific variation in the visual and acoustic displays of wild ungulates, by adopting a two-pronged approach based on (1) comparative analyses with phylogenetic controls, and (2) playback experiments in the field. Comparative analyses provided the opportunity to test the validity of functional hypotheses proposed to explain the extreme diversity of sexual signals observed across ungulates (Chapter 2 and Chapter 3). Playback experiments, on the other hand, allowed for a fine-scale examination of (i) the adaptive significance of complex vocalizations (Chapter 4); and of (ii) the impact of anthropogenic disturbance on the flexibility of antipredator signalling systems (Chapter 5).

In Chapter 2, I used the comparative method to identify the evolutionary drivers of courtship display complexity in male bovids and cervids. Specifically, I tested the role of multiple selection pressures in shaping the evolution of elaborate gestural signals. I found that the size of gestural repertoires (intended as a proxy for complexity) was positively correlated with the potential for male polygyny, and with the number of sympatric, closely-related heterospecifics. These patterns point to sexual selection and species recognition as the main promoters of complexity in courtship displays. Moreover, my results showed that larger male body mass was associated with smaller gestural repertoires, possibly due to energetic constraints imposed to movements in very large species.

In Chapter 3, I asked why sexual dimorphism in two morphological signalling traits, namely colouration and pelage ornaments, is absent in a large number of highly polygynous bovids, contrary to expectations from sexual selection theory. I therefore tested whether lack of dimorphism could be explained by unsustainable fitness costs of ornamentation from sex-biased predation in species forming social groups containing multiple males and females (“mixed-sex herds”). Supporting this interpretation, I found that morphological dimorphism was promoted by intense male mating competition, but reduced by the propensity of sexual aggregation. Hence my results indicate that social integration in mixed-sex herds likely represents a powerful evolutionary force limiting the acquisition of dimorphic ornaments, in direct contrast with the positive drive exerted by sexual selection.

In Chapter 4, I examined the adaptive value of the complex roaring display of male impala antelopes (*Aepcyeros melampus*). The roaring display is a signal of territorial advertisement, and consists of combinations of snorts and grunts. However, similar snorts are also used in isolation as alarm calls. Using playback experiments, I therefore focused on (i) establishing whether alarm and “advertisement” snorts where indeed the same calls; and on (ii) examining the function of snorts in the roaring display. I found that male impala reacted with similar risk-aversive responses to both alarm and “advertisement” snorts, indicating equivalence in the message conveyed by the two calls (as also supported by acoustic analyses). By contrast, grunts elicited aggressive behaviour. Roaring displays (snorts + grunts) also triggered aggressive reactions; the presence of the snorts, however, decreased the latency of male impala to respond appropriately to the following grunts. This suggests that snorts, which are originally alarm calls, have acquired a secondary role in roaring displays as “attention-grabbing elements” to the grunting component. My results therefore indicate that vocal complexity can also evolve via the co-option of pre-existing calls for secondary, derived functions.

In Chapter 5, I aimed at determining whether human shields against natural predators along the borders of the Maasai Mara National Reserve (Kenya) could have reduced the alarm call responsiveness of two common antelopes, the topi (*Damaliscus lunatus*) and the Thomson’s gazelle (*Eudorcas thomsonii*). Contrary to my predictions, I found that both topi and gazelles showed stronger rather than weaker alert reactions to playbacks of conspecific alarm calls in areas exposed to human disturbance. I propose that this could be explained by the eventual association of alarm calls with low-intensity but unpredictable threats linked with human activities, which require careful evaluation by receivers.

In summary, these four studies highlight how various social, ecological, and anthropogenic factors have contributed to the diversification of ungulate signalling phenotypes, and might provide useful insights to evaluate the effects of global changes on the behaviour of wild ungulate populations.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 MOTIVATIONS AND AIMS OF THE STUDY

Behavioural ecologists have always been fascinated by the variety of animal communication systems: considerable efforts have been dedicated to find adaptive explanations for signal form and function in the 160 years since the publication of "*On the Origin of Species*" by Charles Darwin. Nevertheless, old and new hypotheses are still debated. Why do some animals use complex signals to communicate? And when are certain sensory modalities (e.g. sound, smell, etc.) preferred over others? Finding answers to these questions does not only offer the opportunity to test key assumptions of evolutionary theory, but can also stimulate a more comprehensive understanding of the origin of human language, music, and dance. Moreover, communication is a crucial determinant of inter- and intraspecific relationships, from intrasexual competition, intersexual courtship to predation, and therefore plays a central but underestimated role in influencing population, community, and ecosystem dynamics. In an age of pervasive human alterations of the natural world, improving our knowledge of signalling behaviour might thus better inform conservation strategies.

This study aims at identifying ultimate and proximate drivers of signal diversity, complexity, and flexibility in ungulates. Specifically, comparative analyses and field experiments were used to address the validity of multiple hypotheses proposed to explain: (i) the extreme interspecific variation in male sexual displays and ornaments (Chapter 2&3); (ii) the functional significance of complex vocalizations (Chapter 4); and (iii) the plasticity of antipredator signalling systems in response to human disturbance (Chapter 5).

The Bovidae and the Cervidae represent two species-rich (comprising, respectively, 143 and 47 species) and highly diversified lineages of mammals (Prothero & Schoch 2002; Fernandez & Vrba 2005). Members of these families range in body size from the royal antelope (*Neotragus pygmaeus*; average body mass = 2.2 kg) and southern pudu (*Pudu puda*; average body mass = 9.6 kg) to the gaur (*Bos frontalis*; up to 1500 kg) and moose (*Alces alces*; up to 700 kg), and are found in the Saharan sand seas as well as in equatorial rainforests and on circumpolar Arctic islands (Nowak 1999; MacDonald 2010). They comprise solitary forest dwellers, gregarious nomads forming thousands-strong herds in dryland ecosystems, and a large number of intermediate forms between these two extremes (Leuthold 1977; Janis 2008). Some pair with life-long reproductive partners, while others promiscuously copulate with several different mates on breeding arenas (Bro-Jørgensen 2011). This diversity in morphology, habitat preferences, and social mating systems provides a unique opportunity to identify general patterns of signal evolution which may be applied to other taxonomic groups. As a matter of fact, several authors have successfully employed bovids and cervids to formulate and test broader hypotheses regarding the function of male weaponry (e.g. Bro-Jørgensen 2007; Plard, Bonenfant & Gaillard 2011); the ecological correlates of mating strategies (e.g. Owen-Smith 1977; Bowyer et al. 2020); and the association between body size and dietary specialization (e.g. Jarman 1974; Brashares, Garland & Arcese 2000). I therefore used ungulates as a model study system to investigate the role of different selection regimes in shaping sexual and antipredator signals.

Socio-ecological differences among bovids and cervids are mirrored by a remarkable diversity in communication systems (Walther 1984). Some species almost exclusively rely on olfactory signals, while others heavily utilize the visual and acoustic channels (Kiley 1972; Walther 1984). Bovids and cervids defending territories possess specialized glands for scent marking (facilitating boundary demarcation), which are in turn reduced or absent in non-territorial species (Gosling 1982). Furthermore, while pelage colours are uniform and cryptic in several antelopes and deer, a number of species sport bright ornaments as signals of competitive ability and/or genetic quality (Caro 2009). Morphological displays are best exemplified by the contrasting black-and-white coats of the Nile lechwe (*Kobus megaceros*) and of the blackbuck (*Antilope* *cervicapra*); and by the long hairy fringes of wild sheep and goats, and of the greater kudu (*Tragelaphus strepsiceros*; Schaller 1977; Kingdon 2015; Lovari et al. 2015; Corlatti & Sivieri 2020). A large number of ungulates also broadcast sexual and aggressive messages via loud vocal displays, that can often travel over considerable distances thanks to modifications of the larynx (Reby & McComb 2003; Frey & Gebler 2010). Long-range vocalizations are typical of the rutting behaviour of large deer (Vannoni, Torriani & McElligott 2005; Cap et al. 2008), muskox (*Ovibos moschatus*; Frey, Gebler & Fritsch 2005), impala (*Aepyceros melampus*; Frey et al. 2020), saiga antelope (*Saiga tatarica*; Frey, Volodin & Volodina 2007), and goitered (*Gazella subgutturosa*) and Mongolian gazelles (*Procapra gutturosa*; Frey et al. 2008; Blank, Ruckstuhl & Yang 2014), but profound species-specific divergences are present in the acoustic characteristics. Based on these premises, bovids and cervids offered an ideal setting to determine the evolutionary forces underlying various forms of communication.

Some ungulates visual and vocal signals also reveal a certain degree of complexity. For example, several antelopes and deer employ multi-component gestural displays, corresponding to coordinated movements of the body and appendages, in agonistic and/or sexual contexts (Schaller 1977; Walther 1984). These include the ritualized postures adopted in the territorial contests of the blue wildebeest (*Connochaetes taurinus*) and hartebeest (*Alcelaphus buselaphus*; Estes 1991a), and in the courtship behaviour of the male topi (*Damaliscus lunatus*) and Tibetan antelope (*Pantholops hodgsonii*; Estes 1991a; Schaller 2000). Other species sport multiple sexual ornaments: in male eland (*Taurotragus oryx*), hair tufts and dark face masks both contribute to advertise social status (Bro-Jørgensen & Beeston 2015). Loud vocalizations can also present elaborate structures, with different call components arranged together into sequences and reminiscent of bird song (Reby & McComb 2003; Frey et al. 2020). The complex displays of bovids and cervids could thus allow for novel insights into the adaptive value of elaborate signalling systems.

Finally, ungulates also exhibit a striking behavioural flexibility in response to abrupt changes in environmental conditions (e.g. Brashares & Arcese 2002; Found & St. Clair 2017; Gersick & Rubenstein 2017). Risk-sensitive behaviours are particularly prone to short-term adjustments, and have been widely employed as indicators of the type and level of human disturbance in natural landscapes (e.g. Manor & Saltz 2003; Yamashita et al. 2012; Wevers et al. 2020). Increasing vigilance rates and shifts of activity patterns towards night time, for example, usually reflect active persecution via hunting or human-wildlife conflicts (Brown et al. 2012; Crosmary et al. 2012; Paton et al. 2017). On the other hand, nature-based tourism and urbanization generally result into habituation to people and loss of fearful reactions (Sawyer et al. 2017; Found 2019). Hence the possibility exists that ungulate antipredator signalling systems, as part of risk-sensitive strategies, might also show some degree of plasticity under exposure to humans. This could prove useful in assessing the extent of anthropogenic impacts on animal communication.

1.2 SUMMARY OF THE RESEARCH QUESTIONS

What drives the evolution of complex courtship displays?

Courtship behaviour is characterized by prolonged signal exchanges between males and females, leading up to either copulation or rejection of the partner (Bradbury & Vehrencamp 2011). Gestural displays, involving stereotypic movements of the body or appendages, are typical elements of male courtship in several terrestrial vertebrates, sometimes combined together into spectacular "choreographies" (Bradbury & Vehrencamp 2011; Mitoyen, Wuigley & Fusani 2019; Tobiansky & Fuxjager 2020). Such sophisticated gestures usually convey relevant information to females about male competitive ability and genetic quality (Byers, Hebets & Podots 2010; Barske et al. 2011; Miles & Fuxjager 2018; Mitoyen et al. 2019). Well-known examples include the "dances" of jumping spiders, sticklebacks, lizards, ducks, and birds of paradise (Ord, Blumstein & Evans 2001; Wong, Candolin & Lindström 2007; Kozak & Uetz 2016; Ligon et al. 2018). The single components of gestural courtship displays are highly conservative in shape and function, and thereby easily identifiable across closely-related heterospecifics (e.g. the head-bobbing displays of *Anolis* lizards; Ord et al. 2001). However, the overall gestural repertoires (i.e. the number of display components) present a high level of interspecific variation, with some species engaging into substantially more complex courtship displays than others (Miles, Cheng & Fuxjager 2017; Mitoyen et al. 2019). Such variation is brought to an extreme in bovids and cervids, with repertoires ranging from simple head postures to elaborate gaits requiring the coordinated movements of neck, legs, and tail (Walther 1984; Schaller 2000). Nonetheless, the factors promoting or suppressing gestural complexity remain poorly understood.

Under sexual selection theory, the evolution of increasingly complex displays should be closely correlated with the intensity of male competition over reproductive opportunities (Darwin 1871; Andersson 1994; Ord & Garcia-Porta 2012; Eliason 2018). Individuals performing more elaborate courtship than competitors would attract more females, thereby accruing a higher mating success and likely siring a larger number of offspring (Kirkpatrick 1987; Andersson 1994). The positive drive towards complexity should thus be especially accentuated in polygynous mating systems, where a few males compete to monopolize access to copulations with multiple females (Emlen & Oring 1977; Andersson 1994; Arnold & Duvall 1994). However, recent comparative studies on different bird families did not find any strong associations between gestural complexity in courtship displays and the opportunity for polygynous mating (Ligon et al. 2018; Miles et al. 2017, 2018). A similar pattern also emerges in ungulates, since species sharing similar levels of male polygyny seem equally likely to exhibit either large or small gestural repertoires (Schaller 1977, 2000; Walther 1984). Hence, these observations speak against sexual selection as the sole engine of display elaboration.

Alternatively, complexity in gestural displays might arise as a result of selection pressures for pre-copulatory barriers against interspecific hybridization (Mitoyen et al. 2019; Ota 2020). Richer gestural repertoires allow for greater signal diversification, facilitating species recognition during courtship (Mitoyen et al. 2019). Schaller (1977) and Walther (1984) accordingly noticed that, although single display components may appear similar across ungulates, combinations of the various gestures and postures are highly species-specific and might thus allow females to tell apart conspecific from heterospecific males. In **Chapter 2** of this thesis, I therefore investigated the respective contribution of sexual selection and species recognition in favouring complex gestural displays, by applying the comparative method with phylogenetic controls.

Why is morphological sexual dimorphism absent in several polygynous mammals?

Pronounced sexual dimorphism in body size and weaponry is common across several lineages of mammals, from primates to ungulates and pinnipeds (Lindenfors, Tullberg & Biuw 2002; Perez-Barberia, Gordon & Pagel 2012; Cassini 2020). In some cases, differences between males and females also encompass pelage colour and other putatively ornamental traits, such as manes or beards (Caro 2009). Charles Darwin (1871) first proposed that colourful and flamboyant male appearances were the product of sexual selection for male signalling phenotypes. Subsequent studies have confirmed that male dimorphic colourations and ornaments (here referred to as "morphological dimorphism") primarily function as signals of dominance status in both intra- and inter-sexual interactions (Simmons, Lupold & FitzPatrick 2017; Petersen & Higham 2020; Dixson 2020). For example, the face ridges in mandrill (*Mandrillus sphynx*), the fleshy chest patch in gelada (*Theropithecus gelada*), and the lion (*Panthera leo*) mane, all convey information about male dominance rank and competitive ability, and are carefully assessed during agonistic contests over access to oestrous females, in order to prevent costly fights (West & Packer 2002; Setchell et al. 2008; Bergman, Ho & Beehner 2009). The degree of morphological dimorphism should therefore correlate positively with the intensity of sexual selection. Nonetheless, dimorphism is absent in a very large number of highly polygynous mammals (Caro

2009). Alternative selection regimes might therefore be at play in limiting the acquisition of male ornamentation.

The family Bovidae presents a suitable comparative framework to determine evolutionary constraints on morphological dimorphism. Despite the fact that some of the most exaggeratedly ornamented mammals comes from this family, males and females in several bovids are extremely similar in appearance, leading to a certain degree of “sexual uniformity” (Estes 1991b, 2000). The two sexes appear virtually indistinguishable even in some highly polygynous species, including the southern oryx (*Oryx gazella*) and the blue wildebeest (Estes 2000; Caro 2009). Males and females also show convergent colours and ornaments in many antelopes which otherwise exhibit accentuated sexual differences in horns and body size (Estes 2000). A commonly accepted explanation is that the widespread absence of morphological dimorphism is tightly connected with the type of social organization.

Previous authors noticed that most non-dimorphic, polygynous bovids also formed prolonged associations of multiple males and females or “mixed-sex herds” (Jarman 1983; Estes 1991b). Conversely, distinctive male colours and pelage structures (e.g. manes, beards) seems to be largely restricted to those species with sexes rigidly segregated into distinct social groups outside of the reproductive context (Estes 2000). Following these observations, Jarman (1983) proposed that dimorphic traits might be deleterious in mixed-sex herds, drawing the attention of visually-oriented predators (i.e. relying on sight during hunting) to ornamented adult males. Sexual uniformity would therefore become advantageous against male-biased mortality, as it reduces individual conspicuousness (Landeau & Terborgh 1986). Estes (1991b) further suggested that uniformity could as well contribute to maintain herd cohesion, by limiting male intra-sexual aggression. In **Chapter 3** of this study, I investigated whether the formation of mixed-sex herds has prevented the acquisition of dimorphic male ornaments in bovids, thus counteracting the effects of sexual selection.

Can complexity in vocal displays derive from signal co-option?

A central theme in the study of mammal communication is determining if elaborate vocalizations could derive from combinations of pre-existing calls, in analogy with human language (Townsend et al. 2018; Engesser & Townsend 2019). Call combinations supposedly evolve under selection pressures for signal diversification in species with small and fixed vocal repertoires (Collier et a. 2014; Engesser & Townsend 2019). When combined together, different calls can effectively generate new, emerging messages unrelated to their original information content (Engesser & Townsend 2019; Zuberbuhler 2020). Putty-nosed monkeys (*Cercopithecus nictitans*), for example, concatenate two types of alarm calls into a completely novel sequence which elicits group movement (Arnold & Zuberbuhler 2006). Alternatively, the original message of pre-existing calls can be modified through combinations, thereby acquiring more nuanced “meaning” (Zuberbuhler 2020). This is evident in Campbell’s monkeys (*Cercopithecus campbelli*), where the addition of a suffix decreases the urgency of alarm calls (Ouattara, Lemasson & Zuberbuhler 2009). To date, call combinations have been mostly observed in antipredator signalling systems: but could complex vocal displays of sexual advertisement also originate from similar combinatorial mechanisms?

Although sexual selection has been identified as an active promoter of large vocal repertoires (e.g. Herman et al. 2013; Gustison & Bergman 2016), complex vocal displays in the majority of mammals do not derive from combinations of pre-existing calls (Engesser & Townsend 2019). The “songs” of cetaceans, bats, gibbons, and hyraxes consist of acoustically distinctive components which, although referring to various signaller traits, are meaningless in isolation and only become informative when arranged into sequences (Clarke, Reichard & Zuberbuhler 2006; Suzuki, Buck & Tyack 2006; Kershenbaum et al. 2012; Smotherman et al. 2016). A relevant exception is the use of alarm calls preceding (and sometimes following) loud male vocalizations, during inter- and intra-sexual interactions. Typical examples are found in black-and-white colobus monkeys (*Colobus guereza*; Marler 1972), indri lemur (*Indri indri*; Giacoma et al. 2010), and in a large number of antelopes and deer (Walther 1984; Reby & McComb 2003). The function of these combinations is however still a mystery.

One possible explanation is that emitting alarm calls in the absence of actual predation risk could favour receiver deception in sexual-aggressive contexts. In a study on topi antelope, Bro-Jørgensen and Pangle (2010) found that "false" alarm calls (i.e. not associated with presence of a predator) assisted males in herding females on territories. At the same time, Walther (1984) and Estes (1991a) proposed that alarm calling behaviour during male-male contests could be advantageous at catching opponents off-guard (i.e. by diverting attention to a potential predator), or at deterring intruders from territories (perceived as dangerous). According to this line of thought, alarm calls in complex vocal display might therefore deceptively incite fearful reactions in either females or competitors (or both), to the advantage of the signalling male (Reby & McComb 2003).

Another possibility is that alarm calls in agonistic vocal displays contribute to enhance signal effectiveness. Alarm calls are highly salient (i.e. connected with potential mortality risk) and have evolved for quick attention-grabbing (Fitch, Neubauer & Herzel 2002; Blumstein & Recapet 2009). They might thus serve as "alerting components" (Hebets & Papaj 2005), and increase the salience of the following advertisement vocalizations which contain the relevant sexual-aggressive messages (c.f. Richards 1981 on attention grabbing components in bird song). Co-option of pre-existing signals for secondary, derived functions has been repeatedly proposed as an important pathway to vocal complexity (e.g. Borgia & Coleman 2000; Borgia 2006), but experimental evidence of its occurrence is scarce. Hence in **Chapter 4**, I used playback experiments to identify the signalling role and the potential for co-option of alarm calls in the roaring display of male impala.

Can antipredator signalling systems adjust to human disturbance?

Wild animals exhibit a certain degree of flexibility in communication when exposed to human disturbance (Tuomainen & Candolin 2011; Lowry, Lill & Wong 2013). Birds living in cities modify the timing, duration, and frequency of their songs in order to minimize interferences with background levels of urban noise (Slabbekoorn & Ripmeester 2008; Narango & Rodewald 2018). Cetaceans switch from vocal to visual signals when the acoustic channel is polluted by vessel sounds (Jensen et al. 2009; Dunlop, Cato & Noab 2010). Such plastic adjustments in signalling behaviour are well documented, and usually allow animals to overcome anthropogenic interferences with effective transmission (Tuomainen & Candolin 2011; Berger-Tal et al. 2019). It has also been argued that human disturbance could affect communication more subtly by altering the social and ecological context of signal production (Laiolo 2010; Rosenthal & Stuart-Fox 2012). In particular, it is likely that the disruption of predator-prey interactions due to human expansion into natural habitats might cause a general erosion in the value of antipredator signalling systems (Geffroy et al. 2015; Berger et al. 2020).

Human intervention has led to drastic declines in the abundance of large mammalian carnivores, creating safe refuges for wild ungulates in proximity of human settlements and infrastructures (Berger 2007; Berger et al. 2020). Both bovids and cervids regularly take advantage of these "human shields" against predation risk (Berger 2007; Sarmento, Biel & Berger 2016). In the early 20th century, herds of savannah antelopes would move closer to railways, from which lions had been extirpated (Berger et al. 2020). Female moose with vulnerable calves in modern-day Yellowstone range near highly trafficked motorways, as grizzly bears do not venture there (Berger 2007). Similarly, mountain nyala (*Tragelaphus buxtoni*) in Ethiopia forage and rest in the vicinity of villages at night, reducing their vulnerability to nocturnal predators deterred by human activities (Atickem, Loe & Stenseth 2014). This increasing use of shielded areas where predators are absent or scarce, generally translates into a relaxation of risk-sensitive behaviours (e.g. Shannon et al. 2014; Sarmento & Berger 2017). However, could shielding effects also dampen ungulate responses to antipredator signals, such as alarm calls?

The strength of alarm call responses depends on the level of individual exposure to these signals (Hauser 1988; Magrath, Pitcher & Gardner 2009; Magrath & Bennett 2012). Antelopes and primates, for example, have been found to react less strongly to alarm calls of other species which occur at low densities and are rarely encountered (Cheney & Seyfarth 1994; Kitchen et al. 2010; Meise, Franks & Bro-Jørgensen 2018). In the presence of human shields, alarm calls are expected to be heard less frequently (due to fewer encounters with predators), reducing the opportunity for learning about the associated danger, leading to an overall reduction in responsiveness (Berger et al. 2020). Moreover, alarm calling in shielded areas might also become attached to less serious threats than natural predation (e.g. nuisances caused by humans), thereby further reducing the need for high-intensity responses (Blumstein 2016; Berger et al. 2020).

An attenuation in alarm call responsiveness could provide significant benefits to ungulates under shielding effects, as it would allow individuals to re-allocate time budgets to foraging without incurring into the costs costs deriving from failed predator detection (Blumstein 2016; Geffory et al. 2015). By contrast, low reactivity might become disadvantageous in case human shields are lost, and natural predation regimes are reinstated (Berger et al. 2020). Inexperienced or de-sensitized ungulates in formerly shielded areas might not be able to adequately assess alarm calls and the associated threatening stimuli, thus suffering increasing mortality (Sih et al. 2010; Moseby, Blumstein & Letnic 2016). This could contribute to the population declines often observed following predator re-colonization or reintroduction (Beschta & Ripple 2009; Grange et al. 2012). The potential impacts of human shields on antipredator signals should thus be taken into account by conservation managers while planning for ecosystem restoration. In **Chapter 5** of this thesis, I tested whether alarm call responsiveness in two African antelopes were affected by human disturbance and associated shielding effects.

1.3 STUDY AREA

The field component of this study was conducted in the Maasai Mara National Reserve. The Mara is located in the Narok County of south-western Kenya, along the border with Tanzania (1°20'S, 35°10'E), and covers approximately 1510 km^2 (**Figure 1**). The area was proclaimed as a game reserve in 1961, and is administered by the Narok County Government, except for the Mara Triangle which is currently privately managed under the Mara Conservancy. The reserve is part of the Greater Serengeti-Mara Ecosystem, spanning ~ 25 000 km^2 and traditionally defined by the annual migratory movements of blue wildebeest and plains zebra (*Equus quagga*; Thirgood et al. 2004). The ecosystem encompasses the Serengeti National Park, Ngorongoro Conservation Area, and several game reserves in northern Tanzania; and the Mara and adjoining community conservancies in Kenya. Outside protected areas, human settlements are rapidly expanding, in connection with pastoralism in the northern and eastern regions, and with agricultural developments on the floodplains of Lake Victoria to the west (Løvschal et al. 2017; Veldhuis et al. 2019).

Minimum and maximum daily temperatures average 15.5°C ± 0.4°C and 29.5°C ± 0.5°C (mean ± S.E.; Green et al. 2015), Annual rainfall in the Mara is about 600 mm (Norton-Griffiths, Herlocker & Pennycuick 1975). Approximately 80% of the precipitation occurs between November and May, defining a wet and a dry season (Ogutu et al. 2008; Green et al. 2015). A drier spell, referred to as the "short dry season", might be observed between December and February, but rainfall is still regularly experienced at this time of the year (Ogutu et al. 2008). This study was conducted between September 2017 and May 2018, spanning the entirety of the wet season, and coinciding with a year of exceptionally high rainfall caused by El Nino Southern Oscillation (Ogutu et al. 2008).

The Mara presents an undulated topography, with elevation varying between 1486 and 2149 meters above sea level (Sinclair 1995). Hills and rocky outcrops known as “inselbergs” are found in the East (Sekenani Hills), along the Tanzanian border (Roan Hill, Lookout Hill), and in the north-western area (Rhino Ridge; Sinclair 1995; **Figure 1**). The substrate is mostly constituted by quartzitic gneiss and granites, exposed on inselbergs (Sinclair 1995). Soils are well drained and dominated by black cotton clay, although sandy and lateritic deposits are associated with water erosion in the vicinity of major drainage lines (Sinclair 1995). The reserve is crossed by several watercourses, but only the Mara and, to a lesser extent, the Talek river can be defined as perennial. Although the Talek river may stop flowing during the dry season, it usually holds water in deep pools. A system of wetlands is connected with flat lands in proximity to the Mara river. The most extensive is the Musiara swamp, which retains water and green grass well into the dry season and attracts large numbers of ungulates once the ephemeral waterholes in the surrounding areas have dried out (Sinclair 1995).

Vegetation communities in the Mara largely correspond to open grasslands dotted with *Acacia tortilis* and *Balanites* sp. trees (Sinclair 1995). The dominant grass species is *Themeda triandra*, which is highly nutritious and forms tall swards favoured by migratory herds (McNaughton 1985; Holdo, Holt & Fryxell 2009). High grazing pressures by herbivores often produce short-grass areas, or “grazing lawns”, where *Cynodon dactylon* is the most common herbaceous species (McNaughton 1985). These lawns offer frequent green re-growth and are thus attractive to selective feeders, such as Thomson’s gazelles (*Eudorcas thomsonii*) and warthog (*Phacochoerus aethiopicus*; McNaughton 1985). Grasslands are dotted with patchy thickets of *Acacia drepanolobium* and *Croton dichogamus*, sometimes forming relatively dense stands (Sinclair 1995). Broad-leaved *Combretum zeyheri* and *Terminalia sericea* woodlands, on the other hand, characterize hilly areas (Sinclair 1995). Gallery forests are found along the Mara and Talek rivers, often extending up to several hundred meters from the banks. These communities feature very large fig trees (*Ficus* sp. Sinclair 1995). Thickets, woodlands, and forests provide suitable forage for browsing and mixed-feeding herbivores (i.e. consuming both woody and herbaceous plants), such as giraffe (*Giraffa camelopardlis*), eland, and impala (Pellew 1983). Wetlands are characterized by seasonally or permanently waterlogged grasslands and stands of reeds sought after by tall-grass grazers (e.g. buffalo *Syncerus caffer*, elephant *Loxodonta africana*; McNaughton 1985).

Large numbers of wildebeest and zebra usually reach the Mara from the Serengeti National Park in the early dry season (June-August), and leave as the first rain starts (October-November; Sinclair 1995; Holdo et al. 2009). In addition to the migratory species, the Mara protects abundant populations of resident wild ungulates, including: topi, Thomson’s gazelle, Grant’s gazelle (*Nanger granti*), impala, hartebeest, waterbuck (*Kobus ellipsiprymnus*), Cape buffalo, giraffe, and warthog. Among other herbivores, elephants, have re-colonized the area after near-extirpation due to commercial ivory hunting, and are now present at high densities (Dublin & Douglas-Hamilton 1987; Morrison et al. 2018). On the other hand, the black rhinoceros (*Diceros bicornis*) population has been reduced to very low numbers (<30 individuals) due to poaching, and has not recovered yet (Walpole et al. 2001). Hippopotamus (*Hippopotamus amphibious*) represent the most common herbivores near perennial rivers. Among large predators, spotted hyenas (*Crocuta crocuta*) outnumber all other carnivores and, although opportunistic, probably represent an important source of mortality for medium-sized antelopes (Holekamp et al. 1997; Farr et al. 2019). Lion (*Panthera leo*) and cheetah (*Acinoyx jubatus*) occur at some of the highest densities on the African continent, presumably due to the wide availability of preferred prey (respectively, wildebeest/zebra and gazelles; Ogutu & Dublin 2002; Broekhuis & Golapaswamy 2016). Leopard (*Panthera pardus*) are also present, but population size is unknown (Sinclair 1995). In the rivers and swamps, Nile crocodiles (*Crocodylus niloticus*) feed on antelopes coming to drink or attempting to cross during migrations.

1.4 STUDY SPECIES

The field study focused on three abundant bovids which of the Mara, namely the impala, topi, and Thomson's gazelle. Here I provide a brief account of the behaviour and ecology of these three antelopes, with a focus on their social and mating systems.

Impala

The impala (**Fig. 2A**) is a medium-sized, gregarious antelope found across East and southern Africa, presenting a pronounced sexual dimorphism – males are heavier than females and horned (male body mass: 53-76 kg; female body mass: 40 – 53 kg; Estes 1991a). The phylogenetic position of this species has been disputed, but recent molecular analyses place it as a sister-taxon to the tribe Alcelaphini (which includes wildebeest, hartebeest, and topi; Fernandez & Vrba 2005). Impalas are classified as "mixed-feeders", switching from a grass-dominated to a browse-dominated diet according to seasonal variations in the quality of forage (Estes 1991a; Kingdon 2015). Therefore, they predominantly inhabit savannah-grassland ecotones where both herbaceous and woody plants are available year-round (Estes 1991a). In the Serengeti-Mara ecosystem, impala graze in relatively open savannah areas during the wet season, but concentrate in the forests and thickets along drainage lines during drier periods (Jarman 1979).

Impala reproduce year-round in East Africa, but there are seasonal fluctuations in the intensity of mating activities (Jarman 1979). Adult males (>3.5 years old) defend breeding territories against intruders of the same sex, but the territorial network breaks down during the driest months of the year (June-August; Jarman 1979). Females live in loose herds with juvenile males, and visit male territories which contain relevant forage resources (Jarman & Jarman 1973). Births peak in February-April, and lambs remain hidden for a week or less before joining nursery herds (Estes 1991a; Jarman 1979). Young males are evicted from the natal herd and become part of bachelor herds at 8 months of age (Jarman 1979). The bachelor society also include adult males recently evicted from territories (Jarman & Jarman 1973; Jarman 1979). Bachelors form dominance hierarchies, and top-ranking individuals in a herd would then challenge other males for territorial status (Jarman 1979). Adult impala are mainly vulnerable to leopard, cheetah, African wild dog (*Lycaon pictus*), and spotted hyena, and less frequently killed by lion. A variety of smaller carnivores pose a threat to lambs (Estes 1991a, Kingdon 2015).

Impala exhibit a relatively larger repertoire of vocalizations than other antelopes. Jarman (1979) in a long term study of the Serengeti population, described (i) snorts, emitted as alarm calls by both sexes, and during male-male aggressive interactions; (ii) a male roaring display of sexual-aggressive advertisement, consisting of combinations of snorts and grunts; (ii) a sneezing courtship call; (iv) a female-lamb "contact call"; and (v) a distress call, usually emitted by lambs in dangerous situations. The roaring display (the main focus of my investigations), has been classified as an acoustic signal of territorial status, as it is generally produced by males actively defending a territory (Jarman 1979; Frey et al. 2020). Non-territorial males, on the other hand, only engage into roaring displays during episodes of "mass-roaring" connected with high arousal and excitement (e.g. a fight between neighbouring territorial males; Jarman 1979).

Topi

The topi (**Fig. 2B**) is a relatively large gregarious antelope (male: 111 – 147 kg; female: 90 - 130 kg) of the Alcelaphini tribe (Estes 1991a). Horns are present in both sexes. Populations of topi are widely distributed across African savannah ecosystems north and south of the Equator, in open or lightly wooded grasslands (Estes 1991a; Kingdon 2015). Topi are selective grazers with a preference for green grass blades (Murray

1993), and are thus almost exclusively restricted to areas receiving relatively high rainfall or periodic flooding (Kingdon 2015). Wherever prolonged dry seasons cause a shortage of green grass, such as in the Nile floodplains of South Sudan, long-range seasonal movements occur in search of adequate forage (Morjan et al. 2018). In the Mara, topi are largely sedentary and occupy home ranges smaller than 7 km^2 (Bro-Jørgensen 2003).

Adult male topi usually defend breeding territories which are visited by oestrous females during the mating season (Bro-Jørgensen 2008). Males sometimes aggregate on breeding arenas or “leks”, where females compete to copulate with males holding central locations (Bro-Jørgensen 2002). Topi are strictly seasonal breeders and 90% of calves are conceived in a 1.5 month oestrous falling between March and May in the Mara (Estes 1991a; Bro-Jørgensen 2002). Calves lie out in the open and follow their mothers soon after birth, reaching sexual maturity and adult size at two (females) or three (males) years old (Estes 1991a). However, males do not usually reproduce before gaining territorial status (> 4 years old), and join bachelor herds before acquiring a territory (Estes 1991a). Outside of the mating season, multiple males and females form large mixed-sex herds (Estes 1991a). Major predators of the topi include lion, spotted hyena, leopard, cheetah, and African wild dog, with black-backed jackals (*Canis mesomelas*) occasionally killing calves (Estes 1991a).

Thomson’s gazelle

The Thomson’s gazelle (**Fig. 2C**) is the smallest antelope in the tribe Antilopini (males = 17 – 29 kg; females = 13 – 23.5 kg; Estes 1991a). Although horns are present in both sexes, males exhibit significantly longer and thicker horns than females (Estes 1991a). Its distribution is restricted to the grasslands of central-southern Kenya and northern Tanzania (Estes 1991a; Kingdon 2015). Gazelles are mixed-feeders and invariably graze and browse, although generally favouring short, green grasses (Estes 1991a). In the Serengeti-Mara ecosystem, some gazelles engage into long-distance migrations following local rainfall patterns, while others appear to be mostly sedentary (Durant et al. 1988). The diameter of home ranges varies from 1 to 3 km^2 in resident sub-populations, but the actual extent of migratory movements is largely unknown (Estes 1991a).

Female gazelles live in loose aggregations, with no lasting ties except between mothers and their offspring (Estes 1991a). Adult males occupy either permanent or temporary breeding territories, with the latter usually vacated during migrations (Walther 1978). Mating occurs over an extended breeding period in East Africa, coinciding with the wet season (Estes 1991a). Fawns remain hidden for a minimum of two weeks after birth, and by eight weeks are fully capable of following their mothers (Estes 1991a). Young males join bachelor herds at 8 months of age (Estes 1991a), and are sexually mature by 15 months, but age at first reproduction is unknown (Estes 1991a). Gazelles are preyed upon by all large savannah carnivores, but represent preferred dietary items only for cheetah, leopard, and African wild dog (Estes 1991a). Black-backed jackal kill both adults and fawns, which also fall victim to birds of prey and large snakes (Estes 1991a).

1.5 FIGURES

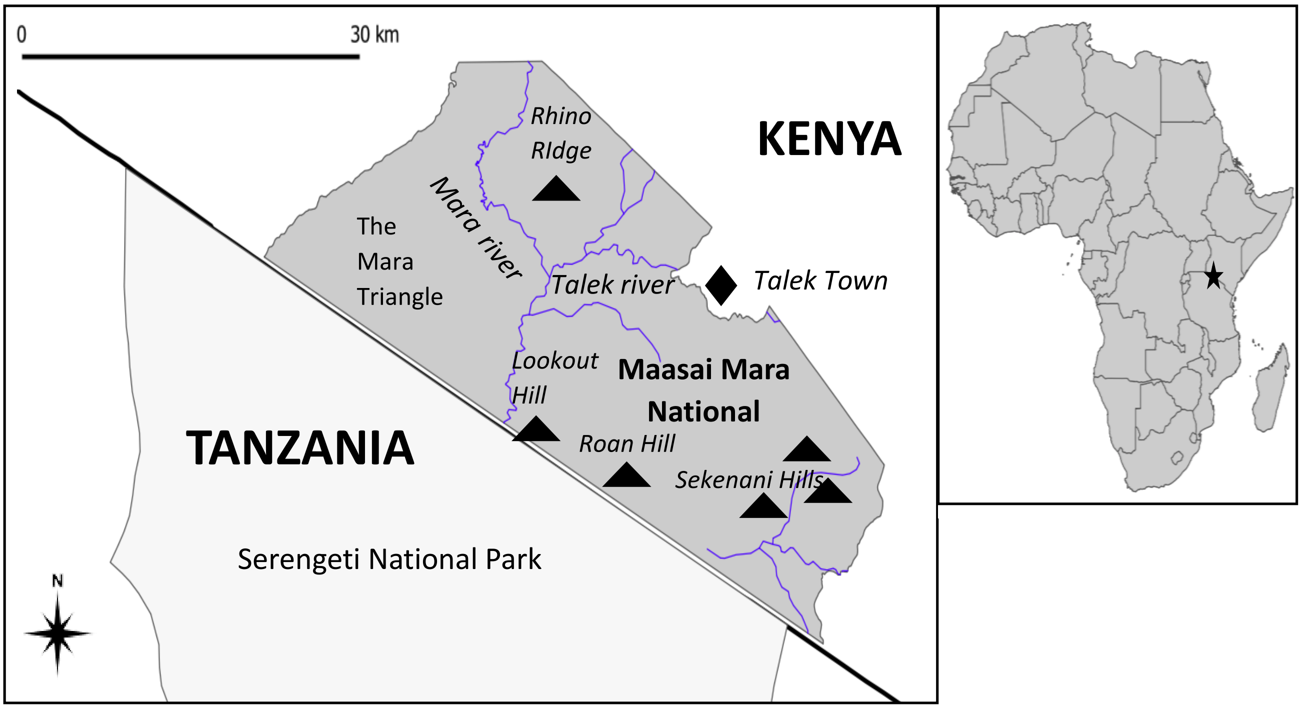


Figure 1: Map of the Maasai Mara National Reserve, with prominent topographic features including rivers, hills, and main human settlements.

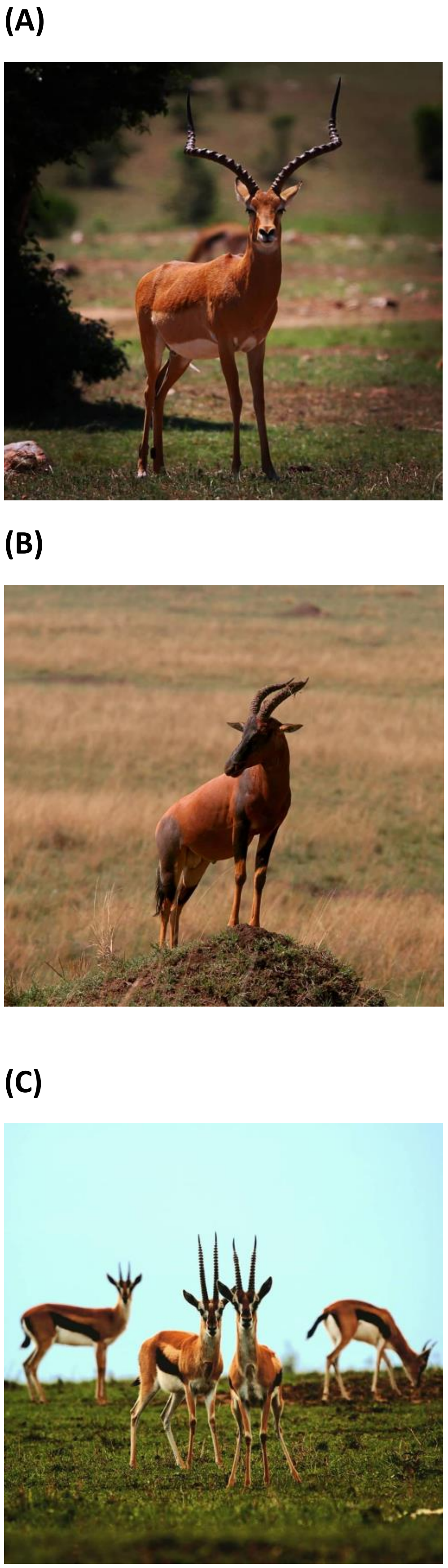


Fig. 2: Images of study species: (A) impala (male); (B) topi (male); (C) Thomson’s gazelle (males).

1.6 REFERENCES

Andersson, M. (1994). *Sexual selection*. Princeton University Press.

Arnold, S. J., & Wade, M. J. (1984). On the measurement of natural and sexual selection theory. *Evolution*, **38**(4), 709-719.

Arnold, S. J., & Duvall, D. (1994). Animal mating systems: a synthesis based on selection theory. *The American Naturalist*, **143**(2), 317-348.

Arnold, K., & Zuberbühler, K. (2006). Semantic combinations in primate calls. *Nature*, **441**(7091), 303-303.

Atickem, A., Loe, L. E., & Stenseth, N. C. (2014). Individual heterogeneity in use of human shields by mountain nyala. *Ethology*, **120**(7), 715-725.

Barske, J., Schlinger, B. A., Wikelski, M., & Fusani, L. (2011). Female choice for male motor skills. *Proceedings of the Royal Society B: Biological Sciences*, **278**(1724), 3523-3528.

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, **3**(6), 620-623.

Berger, J., Wangchuk, T., Briceno, C., Vila, A., & Lambert, J. E. (2020). Disassembled Food Webs and Messy Projections: Modern Ungulate Communities in the Face of Unabating Human Population Growth. *Frontiers in Ecology and Evolution*, **8**, 128.

Berger-Tal, O., Wong, B. B., Candolin, U., & Barber, J. (2019). What evidence exists on the effects of anthropogenic noise on acoustic communication in animals? A systematic map protocol. *Environmental Evidence*, 8(1), 1-7.

Bergman, T. J., Ho, L., & Beehner, J. C. (2009). Chest color and social status in male geladas (*Theropithecus gelada*). *International Journal of Primatology*, **30**(6), 791-806.

Beschta, R. L., & Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, **142**(11), 2401-2414.

Blank, D. A., Ruckstuhl, K., & Yang, W. (2014). Roaring function in male goitered gazelles. *Behavioural Processes*, **106**, 152-159.

Blumstein, D. T. (2016). Habituation and sensitization: new thoughts about old ideas. *Animal Behaviour*, **120**, 255-262.

Blumstein, D. T., & Recapet, C. (2009). The sound of arousal: The addition of novel non-linearities increases responsiveness in marmot alarm calls. *Ethology*, **115**(11), 1074-1081.

Borgia, G. (2006). Preexisting male traits are important in the evolution of elaborated male sexual display. *Advances in the Study of Behavior*, **36**, 249-303.

Borgia, G., & Coleman, S. W. (2000). Co–option of male courtship signals from aggressive display in bowerbirds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **267**(1454), 1735-1740.

Bowyer, R. T., McCullough, D. R., Rachlow, J. L., Ciuti, S., & Whiting, J. C. (2020). Evolution of ungulate mating systems: Integrating social and environmental factors. *Ecology and Evolution*. In Press.

Bradbury, J. W., & Vehrencamp, S. L. (2011). *Animal communication*. Sinauer.

Brashares, J. S., Garland Jr, T., & Arcese, P. (2000). Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. *Behavioral Ecology*, **11**(4), 452-463.

Brashares, J. S., & Arcese, P. (2002). Role of forage, habitat and predation in the behavioural plasticity of a small African antelope. *Journal of Animal Ecology*, **71**(4), 626-638.

Bro-Jørgensen, J. (2002). Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences*, **99**(14), 9290-9293.

Bro-Jørgensen, J. (2003). The significance of hotspots to lekking topi antelopes (*Damaliscus lunatus*). *Behavioral Ecology and Sociobiology*, **53**(5), 324-331.

Bro-Jørgensen, J. (2007). The intensity of sexual selection predicts weapon size in male bovids. *Evolution: International Journal of Organic Evolution*, **61**(6), 1316-1326.

Bro-Jørgensen, J. (2008). The impact of lekking on the spatial variation in payoffs to resource-defending topi bulls, *Damaliscus lunatus*. *Animal Behaviour*, **75**(4), 1229-1234.

Bro-Jørgensen, J. (2011). Intra-and intersexual conflicts and cooperation in the evolution of mating strategies: lessons learnt from ungulates. *Evolutionary Biology*, **38**(1), 28-41.

Bro-Jørgensen, J., & Pangle, W. M. (2010). Male topi antelopes alarm snort deceptively to retain females for mating. *The American Naturalist*, **176**(1), E33-E39.

Bro-Jørgensen, J., & Beeston, J. (2015). Multimodal signalling in an antelope: fluctuating facemasks and knee-clicks reveal the social status of eland bulls. *Animal Behaviour*, **102**, 231-239.

Broekhuis, F., & Gopalaswamy, A. M. (2016). Counting cats: Spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PLoS One*, **11**(5), e0153875.

Brown, C. L., Hardy, A. R., Barber, J. R., Fristrup, K. M., Crooks, K. R., & Angeloni, L. M. (2012). The effect of human activities and their associated noise on ungulate behavior. *PloS one*, **7**(7), e40505.

Byers, J., Hebets, E., & Podos, J. (2010). Female mate choice based upon male motor performance. *Animal Behaviour*, **79**(4), 771-778.

Cap, H., Deleporte, P., Joachim, J., & Reby, D. (2008). Male vocal behavior and phylogeny in deer. *Cladistics*, **24**(6), 917-931.

Caro, T. (2009). Contrasting coloration in terrestrial mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**(1516), 537-548.

Cassini, M. H. (2020). Sexual size dimorphism and sexual selection in primates. *Mammal Reviews*. In Press.

Cheney, D. L., & Seyfarth, R. M. (1994). *How monkeys see the world: Inside the mind of another species*. University of Chicago Press.

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild gibbon songs. *PloS One*, **1**(1), e73.

Collier, K., Bickel, B., van Schaik, C. P., Manser, M. B., & Townsend, S. W. (2014). Language evolution: syntax before phonology?. *Proceedings of the Royal Society B: Biological Sciences*, **281**(1788), 20140263.

Corlatti, L., & Sivieri, S. (2020). Face markings in Northern chamois: cues of dominance? *Mammalian Biology.* In press.

Crosmary, W. G., Makumbe, P., Côté, S. D., & Fritz, H. (2012). Vulnerability to predation and water constraints limit behavioural adjustments of ungulates in response to hunting risk. *Animal Behaviour*, **83**(6), 1367-1376.

Darwin, C. (1871). *The descent of man and selection in relation to sex*. Appleton.

Dixson, B. J. (2020). Introduction to the Special Edition: Intra-Sexual Selection and the Evolution of Male Facial Threat and Dominance Displays. *Adaptive Human Behavior and Physiology*. In Press.

Dublin, H. T., & Douglas-Hamilton, I. (1987). Status and trends of elephants in the Serengeti-Mara ecosystem. *African Journal of Ecology*, **25**(1), 19-33.

Dunlop, R. A., Cato, D. H., & Noad, M. J. (2010). Your attention please: increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae*). *Proceedings of the Royal Society B: Biological Sciences*, **277**(1693), 2521-2529.

Durant, S. M., Caro, T. M., Collins, D. A., Alawi, R. M., & FitzGibbon, C. D. (1988). Migration patterns of Thomson's gazelles and cheetahs on the Serengeti Plains. *African Journal of Ecology*, **26**(4), 257-268.

Eliason, C. M. (2018). How do complex animal signals evolve?. *PLoS Biology*, **16**(12), e3000093.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**(4300), 215-223.

Engesser, S., & Townsend, S. W. (2019). Combinatoriality in the vocal systems of nonhuman animals. *Wiley Interdisciplinary Reviews: Cognitive Science*, **10**(4), e1493.

Estes, R. D. (1991a). *The behaviour guide to African mammals*. The University of California Press.

Estes, R. D. (1991b). The significance of horns and other male secondary sexual characters in female bovids. *Applied Animal Behaviour Science*, **29**(1-4), 403-451.

Estes, R. D. (2000). Evolution of conspicuous coloration in the Bovidae: female mimicry of male secondary sexual characters as a catalyst. In Schaller, G.B., & Vrba, E. S. (Eds). *Antelopes, deer and relatives*. Yale University Press, New Haven & London.

Farr, M. T., Green, D. S., Holekamp, K. E., Roloff, G. J., & Zipkin, E. F. (2019). Multispecies hierarchical modeling reveals variable responses of African carnivores to management alternatives. *Ecological Applications*, **29**(2), e01845.

Fernández, M. H., & Vrba, E. S. (2005). A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. *Biological Reviews*, **80**(2), 269-302.

Fitch, W. T., Neubauer, J., & Herzel, H. (2002). Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour*, **63**(3), 407-418.

Found, R. (2019). Personality influences habituation behaviour in ungulates. *Journal of Ethology*, **37**(1), 47-58.

Found, R., & St. Clair, C. C. (2017). Ambidextrous ungulates have more flexible behaviour, bolder personalities and migrate less. *Royal Society Open Science*, **4**(2), 160958.

Frey, R., Gebler, A., & Fritsch, G. (2006). Arctic roars–laryngeal anatomy and vocalization of the muskox (Ovibos moschatus Zimmermann, 1780, Bovidae). *Journal of Zoology*, **268**(4), 433-448.

Frey, R., Volodin, I., & Volodina, E. (2007). A nose that roars: anatomical specializations and behavioural features of rutting male saiga. *Journal of Anatomy*, **211**(6), 717-736.

Frey, R., Gebler, A., Olson, K. A., Odonkhuu, D., Fritsch, G., Batsaikhan, N., & Stuermer, I. W. (2008). Mobile larynx in Mongolian gazelle: retraction of the larynx during rutting barks in male Mongolian gazelle (*Procapra gutturosa* Pallas, 1777). *Journal of Morphology*, **269**(10), 1223-1237.

Frey, R., & Gebler, A. (2010). Mechanisms and evolution of roaring-like vocalization in mammals. In *Handbook of Behavioral Neuroscience* (Vol. 19, pp. 439-450). Elsevier.

Frey, R., Volodin, I. A., Volodina, E. V., Efremova, K. O., Menges, V., Portas, R., & von Dörnberg, K. (2020). Savannah roars: The vocal anatomy and the impressive rutting calls of male impala (*Aepyceros melampus*)–highlighting the acoustic correlates of a mobile larynx. *Journal of Anatomy*, **236**(3), 398-424.

Geffroy, B., Samia, D. S., Bessa, E., & Blumstein, D. T. (2015). How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology & Evolution*, **30**(12), 755-765.

Gersick, A. S., & Rubenstein, D. I. (2017). Physiology modulates social flexibility and collective behaviour in equids and other large ungulates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **372**(1727), 20160241.

Giacoma, C., Sorrentino, V., Rabarivola, C., & Gamba, M. (2010). Sex differences in the song of Indri indri. *International Journal of Primatology*, **31**(4), 539-551.

Gosling, L. M. (1982). A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie*, **60**(2), 89-118.

Grange, S., Owen-Smith, N., Gaillard, J. M., Druce, D. J., Moleón, M., & Mgobozi, M. (2012). Changes of population trends and mortality patterns in response to the reintroduction of large predators: the case study of African ungulates. *Acta Oecologica*, **42**, 16-29.

Green, D. S., Roloff, G. J., Heath, B. R., & Holekamp, K. E. (2015). Temporal dynamics of the reponses by African mammals to prescribed fire. *The Journal of Wildlife Management*, **79**(2), 235-242.

Gustison, M. L., & Bergman, T. J. (2016). Vocal complexity influences female responses to gelada male calls. *Scientific Reports*, **6**, 19680.

Hauser, M. D. (1988). How infant vervet monkeys learn to recognize starling alarm calls: the role of experience. *Behaviour*, **105**(3), 187-201.

Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, **57**(3), 197-214.

Herman, L. M., Pack, A. A., Spitz, S. S., Herman, E. Y., Rose, K., Hakala, S., & Deakos, M. H. (2013). Humpback whale song: Who sings? *Behavioral Ecology and Sociobiology*, **67**(10), 1653-1663.

Holdo, R. M., Holt, R. D., & Fryxell, J. M. (2009). Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, **173**(4), 431-445.

Holekamp, K. E., Smale, L., Berg, R., & Cooper, S. M. (1997). Hunting rates and hunting success in the spotted hyena (Crocuta crocuta). *Journal of Zoology*, **242**(1), 1-15.

Janis, C. (2008). An evolutionary history of browsing and grazing ungulates. In *The ecology of browsing and grazing* (pp. 21-45). Springer, Berlin, Heidelberg.

Jarman, P. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, **48**(4), 215-267.

Jarman, M. V. (1979). *Impala social behaviour: territory, hierarchy, mating, and the use of space*. Parey.

Jarman, P. (1983). Mating system and sexual dimorphism in large terrestrial, mammalian herbivores. *Biological Reviews*, **58**(4), 485-520.

Jarman, P. J., & Jarman, M. V. (1973). Social behaviour, population structure and reproductive potential in impala. *African Journal of Ecology*, **11**(3-4), 329-338.

Jensen, F. H., Bejder, L., Wahlberg, M., Soto, N. A., Johnson, M., & Madsen, P. T. (2009). Vessel noise effects on delphinid communication. *Marine Ecology Progress Series*, **395**, 161-175.

Kershenbaum, A., Ilany, A., Blaustein, L., & Geffen, E. (2012). Syntactic structure and geographical dialects in the songs of male rock hyraxes. *Proceedings of the Royal Society B: Biological Sciences*, **279**(1740), 2974-2981.

Kiley, M. (1972). The vocalizations of ungulates, their causation and function. *Zeitschrift für Tierpsychologie*, **31**(2), 171-222.

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

Kirkpatrick, M. (1987). Sexual selection by female choice in polygynous animals. *Annual Review of Ecology and Systematics*, **18**, 43-70.

Kitchen, D. M., Bergman, T. J., Cheney, D. L., Nicholson, J. R., & Seyfarth, R. M. (2010). Comparing responses of four ungulate species to playbacks of baboon alarm calls. *Animal Cognition*, **13**(6), 861-870.

Kozak, E. C., & Uetz, G. W. (2016). Cross-modal integration of multimodal courtship signals in a wolf spider. *Animal Cognition*, **19**(6), 1173-1181.

Laiolo, P. (2010). The emerging significance of bioacoustics in animal species conservation. *Biological Conservation*, **143**(7), 1635-1645.

Landeau, L., & Terborgh, J. (1986). Oddity and the ‘confusion effect’in predation. *Animal Behaviour*, **34**(5), 1372-1380.

Leuthold, W. (1977). *African ungulates: a comparative review of their ethology and behavioral ecology* (Vol. 8). Springer Science & Business Media.

Ligon, R. A., Diaz, C. D., Morano, J. L., Troscianko, J., Stevens, M., Moskeland, A., & Scholes III, E. (2018). Evolution of correlated complexity in the radically different courtship signals of birds-of-paradise. *PLoS Biology*, **16**(11), e2006962.

Lindenfors, P., Tullberg, B. S., & Biuw, M. (2002). Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology*, **52**(3), 188-193.

Lovari, S., Fattorini, N., Boesi, R., & Bocci, A. (2015). Male ruff colour as a rank signal in a monomorphic-horned mammal: behavioural correlates. *The Science of Nature*, **102**(7-8), 39.

Løvschal, M., Bøcher, P. K., Pilgaard, J., Amoke, I., Odingo, A., Thuo, A., & Svenning, J. C. (2017). Fencing bodes a rapid collapse of the unique Greater Mara ecosystem. *Scientific Reports*, **7**(1), 1-7.

Lowry, H., Lill, A., & Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biological reviews*, **88**(3), 537-549.

Macdonald, D. W. (Ed.). (2010). *The encyclopedia of mammals*. Oxford University Press.

Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2009). Recognition of other species' aerial alarm calls: speaking the same language or learning another?. *Proceedings of the Royal Society B: Biological Sciences*, **276**(1657), 769-774.

Magrath, R. D., & Bennett, T. H. (2012). A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring heterospecifics. *Proceedings of the Royal Society B: Biological Sciences*, **279**(1730), 902-909.

Marler, P. (1972). Vocalizations of East African monkeys II: black and white colobus. *Behaviour*, **42**(3-4), 175-197.

Manor, R., & Saltz, D. (2003). Impact of human nuisance disturbance on vigilance and group size of a social ungulate. *Ecological Applications*, **13**(6), 1830-1834.

McNaughton, S. J. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, **55**(3), 259-294.

Meise, K., Franks, D. W., & Bro-Jørgensen, J. (2018). Multiple adaptive and non-adaptive processes determine responsiveness to heterospecific alarm calls in African savannah herbivores. *Proceedings of the Royal Society B: Biological Sciences*, **285**(1882), 20172676.

Miles, M. C., Cheng, S., & Fuxjager, M. J. (2017). Biogeography predicts macro-evolutionary patterning of gestural display complexity in a passerine family. *Evolution*, **71**(5), 1406-1416.

Miles, M. C., & Fuxjager, M. J. (2018). Animal choreography of song and dance: a case study in the Montezuma oropendola, Psarocolius montezuma. *Animal Behaviour*, **140**, 99-107.

Miles, M. C., Schuppe, E. R., Ligon IV, R. M., & Fuxjager, M. J. (2018). Macroevolutionary patterning of woodpecker drums reveals how sexual selection elaborates signals under constraint. *Proceedings of the Royal Society B: Biological Sciences*, **285**(1873), 20172628.

Mitoyen, C., Quigley, C., & Fusani, L. (2019). Evolution and function of multimodal courtship displays. *Ethology*, **125**(8), 503-515.

Morjan, M. D., Rayl, N. D., Elkan, P. W., Deutsch, J. C., Henke, M. B., & Fuller, T. K. (2018). Armed conflict and development in South Sudan threatens some of Africa's longest and largest ungulate migrations. *Biodiversity and conservation*, **27**(2), 365-380.

Morrison, T. A., Estes, A. B., Mduma, S. A., Maliti, H. T., Frederick, H., Kija, H., & Kohi, E. M. (2018). Informing aerial total counts with demographic models: population growth of Serengeti elephants not explained purely by demography. *Conservation Letters*, **11**(3), e12413.

Moseby, K. E., Blumstein, D. T., & Letnic, M. (2016). Harnessing natural selection to tackle the problem of prey naïveté. *Evolutionary Applications*, **9**(2), 334-343.

Murray, M. G. (1993). Comparative nutrition of wildebeest, hartebeest and topi in the Serengeti. *African Journal of Ecology*, **31**(2), 172-177.

Narango, D. L., & Rodewald, A. D. (2018). Signal information of bird song changes in human-dominated landscapes. *Urban Ecosystems*, **21**(1), 41-50.

Norton-Griffiths, M., Herlocker, D., & Pennycuick, L. (1975). The patterns of rainfall in the Serengeti ecosystem, Tanzania. *African Journal of Ecology*, **13**(3), 347-374.

Nowak, R. M. (1999). *Walker's Mammals of the World*. Johns Hopkins University Press.

Ogutu, J. O., & Dublin, H. T. (2002). Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. *African Journal of Ecology*, **40**(2), 120-129.

Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., & Reid, R. S. (2008). El Niño-southern oscillation, rainfall, temperature and normalized difference vegetation index fluctuations in the Mara-Serengeti ecosystem. *African Journal of Ecology*, **46**(2), 132-143.

Ord, T. J., Blumstein, D. T., & Evans, C. S. (2001). Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**(1468), 737-744.

Ord, T. J., & Garcia-Porta, J. (2012). Is sociality required for the evolution of communicative complexity? Evidence weighed against alternative hypotheses in diverse taxonomic groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**(1597), 1811-1828.

Ota, N. (2020). Tap dancers in the wild: field observations of multimodal courtship displays in socially monogamous songbirds. *The Science of Nature*, **107**(4), 1-5.

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's monkeys use affixation to alter call meaning. *PloS One*, **4**(11), e7808.

Owen-Smith, N. (1977). On territoriality in ungulates and an evolutionary model. *The Quarterly Review of Biology*, **52**(1), 1-38.

Paton, D. G., Ciuti, S., Quinn, M., & Boyce, M. S. (2017). Hunting exacerbates the response to human disturbance in large herbivores while migrating through a road network. *Ecosphere*, **8**(6), e01841.

Pellew, R. A. (1983). The giraffe and its food resource in the Serengeti. I. Composition, biomass and production of available browse. *African Journal of Ecology*, **21**(4), 241-267.

Pérez-Barbería, F. J., Gordon, I. J., & Pagel, M. (2002). The origins of sexual dimorphism in body size in ungulates. *Evolution*, **56**(6), 1276-1285.

Petersen, R. M., & Higham, J. P. (2020). The Role of Sexual Selection in the Evolution of Facial Displays in Male Non-human Primates and Men. *Adaptive Human Behavior and Physiology*. In Press.

Plard, F., Bonenfant, C., & Gaillard, J. M. (2011). Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver. *Oikos*, **120**(4), 601-606.

Prothero, D. R., & Schoch, R. M. (2002). *Horns, tusks, and flippers: the evolution of hoofed mammals*. JHU Press.

Reby, D., & McComb, K. (2003). Vocal communication and reproduction in deer. *Advances in the Study of Behavior*, **33**, 231-264.

Richards, D. G. (1981). Alerting and message components in songs of rufous-sided towhees. *Behaviour*, **76**(3), 223-249.

Rosenthal, G. G. & Stuart-Fox, D., (2012). Environmental disturbance and animal communication. In Candolin, U., & Wong, B. B. (Eds.) *Behavioural responses to a changing world: mechanisms and consequences*, 16-31. Oxford University Press.

Sarmento, W., Biel, M., & Berger, J. B. J. (2016). Redistribution, Human Shields and Loss of Migratory Behavior in the Crown of the Continent. *Intermountain Journal of Sciences*, **22**(4), 118-118.

Sarmento, W. M., & Berger, J. (2017). Human visitation limits the utility of protected areas as ecological baselines. *Biological Conservation*, **212**, 316-326.

Sawyer, H., Korfanta, N. M., Nielson, R. M., Monteith, K. L., & Strickland, D. (2017). Mule deer and energy development—Long-term trends of habituation and abundance. *Global Change Biology*, **23**(11), 4521-4529.

Schaller, G. B. (1977). *Mountain monarchs. Wild sheep and goats of the Himalaya*. University of Chicago Press.

Schaller, G. B. (2000). *Wildlife of the Tibetan steppe*. University of Chicago Press.

Setchell, J. M., Smith, T., Wickings, E. J., & Knapp, L. A. (2008). Social correlates of testosterone and ornamentation in male mandrills. *Hormones and Behavior*, **54**(3), 365-372.

Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS One*, **9**(4), e94630.

Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., & Vonesh, J. R. (2010). Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, **119**(4), 610-621.

Simmons, L. W., Lüpold, S., & Fitzpatrick, J. L. (2017). Evolutionary trade-off between secondary sexual traits and ejaculates. *Trends in Ecology & Evolution*, **32**(12), 964-976.

Sinclair, A. R. E. (1995). Serengeti past and present. In Sinclair, A. R. E., & Arcese, P. (Eds). *Serengeti II: Dynamics, management, and conservation of an ecosystem*, 3-30.

Slabbekoorn, H., & Ripmeester, E. A. P. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular ecology*, **17**(1), 72-83.

Smotherman, M., Knörnschild, M., Smarsh, G., & Bohn, K. (2016). The origins and diversity of bat songs. *Journal of Comparative Physiology A*, **202**(8), 535-554.

Suzuki, R., Buck, J. R., & Tyack, P. L. (2006). Information entropy of humpback whale songs. *The Journal of the Acoustical Society of America*, **119**(3), 1849-1866.

Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., & Borner, M. (2004). Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation*, **7**(2), 113-120.

Tobiansky, D. J., & Fuxjager, M. J. (2020). Sex steroids as regulators of gestural communication. *Endocrinology*. In Press.

Townsend, S. W., Engesser, S., Stoll, S., Zuberbühler, K., & Bickel, B. (2018). Compositionality in animals and humans. *PLoS Biology*, **16**(8), e2006425.

Tuomainen, U., & Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*, **86**(3), 640-657.

Vannoni, E., Torriani, M. V., & McElligott, A. G. (2005). Acoustic signalling in cervids: a methodological approach for measuring vocal communication in fallow deer. *Cognition, Brain, Behaviour*, **9**, 551-566.

Veldhuis, M. P., Ritchie, M. E., Ogutu, J. O., Morrison, T. A., Beale, C. M., Estes, A. B., & Wargute, P. W. (2019). Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. *Science*, **363**(6434), 1424-1428.

Walpole, M. J., Morgan-Davies, M., Milledge, S., Bett, P., & Leader-Williams, N. (2001). Population dynamics and future conservation of a free-ranging black rhinoceros (*Diceros bicornis*) population in Kenya. *Biological Conservation*, **99**(2), 237-243.

Walther, F. R. (1978). Quantitative and functional variations of certain behaviour patterns in male Thomson's gazelle of different social status. *Behaviour*, **65**(1-2), 212-239.

Walther, F. R. (1984). *Communication and expression in hoofed mammals*. Indiana University Press.

West, P. M., & Packer, C. (2002). Sexual selection, temperature, and the lion's mane. *Science*, **297**(5585), 1339-1343.

Wevers, J., Fattebert, J., Casaer, J., Artois, T., & Beenaerts, N. (2020). Trading fear for food in the Anthropocene: How ungulates cope with human disturbance in a multi-use, suburban ecosystem. *Science of The Total Environment*. In Press.

Wong, B. B., Candolin, U., & Lindström, K. (2007). Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *The American Naturalist*, **170**(2), 184-189.

Yamashita, T., Gaynor, K. M., Kioko, J., Brashares, J., & Kiffner, C. (2018). Antipredator behaviour of African ungulates around human settlements. *African Journal of Ecology*, **56**(3), 528-536.

Zuberbühler, K. (2020). Syntax and compositionality in animal communication. *Philosophical Transactions of the Royal Society B*, **375**(1789), 20190062.

CHAPTER 2: SEXUAL SELECTION AND SPECIES RECOGNITION PROMOTE THE EVOLUTION OF COMPLEX COURTSHIP DISPLAYS IN MALE BOVIDS AND CERVIDS

ABSTRACT

Identifying the evolutionary drivers of complexity in sexual signals is a key issue in the study of animal communication. Among mammals, male bovids and cervids often perform elaborate gestural displays during courtship, consisting of ritualized movements of the body and appendages. However, the underlying causes of interspecific variation in the repertoires of gestural displays remain poorly understood. I therefore applied the comparative method with phylogenetic controls to determine which factors could have either promoted or constrained the size of gestural repertoires, here intended as a proxy for complexity.

I found that gestural display complexity in male bovids and cervids was primarily under sexual selection. Repertoire size correlated positively with breeding group size, an indicator of strong sexual selection on males. Moreover, repertoires were larger in species adopting non-territorial and lek breeding systems rather than resource-based territoriality, likely because the sharing of breeding opportunities among territory owners in the latter leads to weaker male mating competition.

The results also indicated that gestural repertoire size increased with the number of closely-related species occurring in sympatry. This suggests that selection against interspecific hybridization might exert a positive drive towards increasing display complexity, facilitating species recognition during courtship. At the same time, repertoire size appeared to be negatively associated with male body mass, possibly due to the energetic and mechanical constraints imposed to movements in very large species. By contrast, I found no evidence that complex gestural displays have been selected for enhanced signal efficacy in dense habitats.

2.1 INTRODUCTION

Ever since the early observations of Darwin (1871), Lorenz (e.g. 1953, 1958, 1971), and Tinbergen (e.g. 1954a, 1954b), animal ethologists have been fascinated by the remarkable diversity in the suite of visual, acoustic, and olfactory displays employed by males during courtship. A vast amount of empirical and theoretical research has been subsequently devoted to address the function of flamboyant sexual signals (e.g. Møller & Pomiamkowski 1993; Ord & Stuart-Fox 2006; Muniz & Machado 2018; Lupold, Simmons & Grueter 2019). However, the ultimate causes underlying interspecific differences in male courtship behaviour are less well understood (Mitoyen, Quigley & Fusani 2019). In particular, why do some species engage into conspicuously more elaborate courtship displays than others? In this study, I aimed at identifying which factors could explain the extreme variation in the complexity of gestural courtship displays observed across two families of ungulates, the Bovidae and the Cervidae.

Gestural displays, defined as ritualized movements (i.e. with no mechanical function) of the body and appendages, characterize sexual interactions in a variety of taxonomic groups (from fruit flies to birds; e.g. Johnson 2000; Ord, Blumstein & Evans 2002; Fusani et al. 2007; Wong, Candolin & Lindström 2007; Dalziell et al. 2013; Ota, Gahr & Soma 2015; Kozak & Uetz 2016; Ligon et al. 2018; Miles & Fuxjager 2018a, 2018b; Ota 2020). Although rare among mammals (likely due to a greater reliance on olfactory communication; Clutton-Brock 2016; Amo & Bonadonna 2018; Coombes, Stockley & Hurst 2018), they are ubiquitous in the courtship behaviour of male ungulates (Leuthold 1977; Walther 1984). In bovids and cervids, the repertoires of gestural displays vary dramatically from species to species, ranging from simple head postures to distinctive gaits requiring the coordinated movement of neck, legs, and tail (Leuthold 1977; Walther 1984; Schaller 1977, 2000). These two families therefore provided an ideal framework to investigate how different evolutionary forces might have promoted or constrained display elaboration.

According to sexual selection theory, male mating competition favours the evolution of complex sexual signals as advertisements of genetic quality or attractiveness to females (*Sexual Selection hypothesis*; Darwin 1871; Kirkpatrick 1987; Andersson 1994; Mitoyen et al. 2019). Complexity in gestural courtship displays, for example, might reflect quality-related male traits, such as motor skills and coordination abilities (Zahavi 1975; Byers, Hebets & Podos 2010; Barske et al. 2011; Fusani et al. 2014; Fuxjager et al. 2015, 2017). Males performing more elaborate courtships than competitors should therefore be preferred as mating partners by females (Kirkpatrick 1987; Andersson 1994; Byers et al. 2010; Barske et al. 2011; Chen et al. 2012; Mitoyen et al. 2019). Such preferences would lead to a substantial skew in mating success among reproductive males, and ultimately exert a strong directional drive towards increasingly complex displays (Emlen & Oring 1977; Wade & Arnold 1980; Kirkpatrick 1987; Shuster & Wade 2003). Since male mating skew scales positively with the number of available reproductive females (Emlen & Oring 1977; Wade & Arnold 1980; Wade & Shuster 2004), the intensity of sexual selection for courtship display complexity should co-vary with the potential for polygynous breeding (Kirkpatrick 1987; Andersson 1994).

In male bovids and cervids, polygyny is affected by the species-specific strategies adopted by males to secure copulations (Clutton-Brock 1989, 2017; Bro-Jørgensen 2007). A key distinction is between males defending access to areas which contain resources sought after by females (territorial strategy); and non-territorial males which directly defend access to oestrous females, after attaining top-ranking status in a dominance hierarchy (non-territorial strategy; Isvaran 2005; Bro-Jørgensen 2007). Territoriality implies a reduction in polygyny, as females typically range over multiple territories and force rivals to share breeding opportunities (Isvaran 2005; Bro-Jørgensen 2007). This would attenuate the strength of sexual selection for elaborate courtship displays in respect to non-territorial species (characterized by higher levels of polygyny; Bro-Jørgensen 2007, 2011). An exception might be represented by lek-based territorial systems, where males congregate on arenas that do not contain relevant resources (Höglund & Alatalo 1995). Oestrous females visiting leks preferentially cluster on certain individual territories (Clutton-Brock, Deutsch & Neftd 1993; Bro-Jørgensen 2002): hence mating success is severely biased in favour of a small number of males holding attractive positions (Apollonio et al. 1992; McComb & Clutton-Brock 1994; Isvaran & Jhala 2000; Bro-

Jørgensen 2002). Contrary to resource-based territoriality, lekking might therefore operate as a catalyst for the evolution of display complexity.

Another possibility is that complex courtship displays have evolved under selection pressures for conspecific mate recognition (*Species Recognition hypothesis*; Ord & Stamps 2009; Bradbury & Vehrencamp 2011; Hill 2015; Mitoyen et al. 2019; Ota 2020). Given the high costs of hybridization (e.g. low offspring viability, miscarriages), male sexual signals are expected to diverge among species that can interbreed, thereby allowing females to reject unsuitable heterospecific partners (Kirkpatrick 1982; Grant & Grant 1997; Hoskin & Higgie 2010; Rosenthal 2013; Scholes & Laman 2018). Nevertheless, the chances for divergence are finite, especially when several closely-related species co-exist in sympatry (Ord, King & Young 2011; Freeberg, Dunbar & Ord 2012; Miles, Goller & Fuxjager 2018). These limitations could be overcome via the addition of novel elements to the available repertoire, which multiply the potential for diversification and allow for generating new signals through combinations (Freeberg et al. 2012; Taylor & Ryan 2013; Hill 2015; Miles, Cheng & Fuxjager 2017). Since hybridization has been widely documented in both bovids and cervids under natural conditions (e.g. Robinson et al. 2015; vaz Pinto et al. 2016), the drive for complex courtship displays might be particularly powerful in these lineages.

Complexity in sexual signalling systems could also reflect adaptations to maximize the efficacy of information transfer (*Signal Efficacy hypothesis*; Candolin 2003; Munoz & Blumstein 2012; Partan 2013, 2017). Conspicuous, multi-component gestural displays often enhance signal detection and discrimination by receivers under sub-optimal conditions for visual communication (i.e. low-lighting, obstruction from vegetation; Ord, Blumstein & Evans 2002; Heindl & Winkler 2003; Doucett, Mennill & Hill 2007; Munoz & Blumstein 2012). Examples include the "attention-grabbing" gestures and postures of terrestrial vertebrates living in thick understorey (e.g. *Anolis* lizards, manakins, and birds of paradise; Ord & Stamps 2008; Fuxjager & Schlinger 2015; Miles & Fuxjager 2018b). Based on these premises, it is thus possible that dense habitats might have selected for complex gestural displays in the courtship behaviour of forest-dwelling bovids and cervids.

I applied the comparative method with phylogenetic controls to address the validity of the three evolutionary hypotheses discussed above (Sexual Selection, Species Recognition, Signal Efficacy). Following previous authors, I used the repertoire of gestural displays (i.e. the overall number of ritualized gestures) as a measure of courtship display complexity (cf. Ord, Blumstein & Evans 2001; Ligon et al. 2018; Miles & Fuxjager 2018b). Under the Sexual Selection hypothesis, I expected that gestural repertoire size would be positively correlated with breeding group size, an indicator of the level of male polygyny (Bro-Jørgensen 2007a; Cassini 2020). I also predicted larger repertoires in species adopting non-territorial and lek mating strategies rather than resource-based territoriality, as the latter entails a reduction in the potential for polygynous mating (due to shared breeding opportunities among territory owners). Under the Species Recognition hypothesis, gestural display complexity was predicted to increase with the number of closely-related species in sympatry ("degree of sympatry" from now onwards), which usually provides a good approximation for hybridization risk (cf. Santana et al. 2012, 2013). Finally, according to the Signal Efficacy hypothesis, dense habitats should promote display complexity in order to prevent signal degradation. I therefore expected a negative correlation between gestural repertoire size and habitat openness. I further tested for an association between repertoire size and body mass, since large size might impose energetic costs on movements and restrict the ability to perform elaborate gestural displays (Taylor et al. 1982). Hypotheses and predictions are summarized in **Table 1**.

2.2 METHODS

Scoring gestural display complexity

Data on gestural courtship displays was collected for 73 bovid and 21 cervid species. Despite the incomplete nature of the dataset, owing mainly to the fact that courtship behaviour has never been formally described in several species, the sample was considered as representative of overall diversity since it included at least one species of each recognized genus, except the poorly known *Pseudoryx* (Bininda-Emonds et al. 2007). Domesticated species were excluded from the study, given the potential for human intervention to have modified behavioural traits. For *Bos frontalis B. grunniens*, and *Capra hircus*, the non-domesticated subspecies, respectively *B. frontalis gaurus*, *B. grunniens mutus*, and *C. hircus aegagrus* were considered for analyses.

Estimates of signal repertoires derived from available descriptions in literature have been successfully applied as proxies for signal complexity in comparative studies (e.g. Ord & Blumstein 2002; Dunn & Smaers 2018; Miles & Fuxjager 2018b). Here I therefore adopted a similar approach and, in order to be as systematic as possible, I applied a series of rules to calculate gestural repertoire size. Peer-reviewed publications and authoritative books in English, French, German, Italian, and Spanish, were surveyed for ethograms detailing the courtship behaviour of bovids and cervids. Only sources which reported a full sequence of inter-sexual interactions leading to copulations were taken into account for data collection.

Gestural repertoire size for each study species was scored as the sum of distinctive movements of the body and appendages, here referred to as “display components”, performed by males during courtship (Appendix I). The classification of display components was based on the seminal work of F.R. Walther (1974, 1984). Definitions also mirrored those provided by Walther (Appendix I). Display components could be broadly divided into four categories reflecting the different body parts involved in the action: (i) head and neck; (ii) forelegs; (iii) hind legs; and (iv) tail. When gestural displays occurred simultaneously on different body parts, they were scored as independent components, since movements of single parts are largely independent from each other (Walther 1984). In case the same component was repeated at various stages of courtship behaviour, or in combination with other components, it was scored as present only once. The full list of display components is provided in Appendix I, while references are provided in Appendix II.

Display components that had not been consistently described across different species were conservatively excluded from calculations. These included head-nodding/jerking, and ear and horn orientation. These displays primarily represent subtle modifiers of other movements (i.e. head-up and low-stretch postures; Walther 1984), and went probably unreported in the majority of ethograms. Executive behaviours, which do not constitute visual signals but serve to accomplish other functions, were also not scored as display components (following indications by Walther 1984). These included: licking, smelling, grooming, and naso-genital contact with associated Flehmen response (all involved in the olfactory investigation of sexual receptivity).

A small number of displays consisted of movements of several body parts which were unlikely to constitute independent signals, but rather mechanical actions aimed at facilitating the expression of a dominant element (e.g. squatting during erectile displays; Walther 1984; Schaller 2000). These were therefore considered as “combined displays” (Appendix I), and each was scored as a single element; I then conducted statistical analyses were with and without adding them to the final gestural repertoire score, and obtained qualitatively similar results (not shown here).

Independent variables

Average male body mass (in kg) and breeding group size in bovids and cervids were extracted from sources listed in Appendix III. Based on available information (Appendix III), male mating strategy was classified as: (i) resource defence territoriality; (ii) lek territoriality; and (iii) non-territoriality (Appendix II). Mating strategy matched the strategy of the population for which gestural repertoire size was calculated.

Habitat openness was scored as the probability of detection for terrestrial mammals in each of the seven main habitat categories in the IUCN Red List classification scheme (www.iucnredlist.org), according to Stankowich & Campbell (2016): (i) 0.1 tropical rainforest; (ii) 0.2 temperate forest; (iii) 0.3 wetland; (iv) 0.5 shrubland; (v) 0.7 grassland (tropical and temperate); (vi) 0.8 rocky areas; and (vii) 0.95 deserts. Scores were assigned only to habitats reported as “suitable”. The average of detection probabilities across all habitat categories was taken as the overall species-specific habitat openness score.

The degree of sympatry with closely-related species was considered as the number of heterospecifics in the same tribe overlapping in distribution range. Bovid and cervid tribes reflected those proposed by Vrba & Schaller (2000), which corresponded to monophyletic groups in the phylogeny adopted here (Bininda-Emonds et al. 2007). I did not limit the scoring of degree of sympatry to co-generic species: among bovids, interspecific hybridization is observed also between species not formally assigned to the same genus (e.g. Jorge, Butler & Benirschke 1976; Douglas et al 2011). Therefore, sharing the same tribal-level classification was considered as representative of the effective potential for hybridization in natural populations. Overlap in geographic distribution was visually estimated by plotting distribution polygons for all species against each of the heterospecifics in the same tribe, using QGIS 3.4.3 (QGIS Development Team 2019). Any observable overlap in geographic range was considered as evidence for sympatry (Santana et al. 2013). Polygons of distribution range were obtained from the IUCN Red List database (www.iucnredlist.org). Although IUCN maps only show current geographic distribution, spatial data on historical occurrence is unavailable or at best largely incomplete for many of the species included in this study. Hence I opted to consistently score the degree of sympatry based exclusively on current distribution ranges.

I also considered the possibility that the gestural repertoire size calculated from literature may have been spuriously affected by differences in research effort between species (e.g. well-studied species would also exhibit larger repertoires). I therefore controlled for research effort by estimating the number of publications mentioning each species (using the Linnean binomial name) in the ISI Web of Knowledge (www.webofknowledge.com) between 1960 and 2018. The search was restricted to the categories which were likely to include behavioural accounts, i.e. (i) Zoology; (ii) Behavioural Sciences; (iii) Ecology; and (iv) Evolutionary Biology.

Statistical analyses

All analyses were conducted in R v. 3.5.2 (R Development Core Team 2019) with the packages ape and caper loaded in the main workspace (Orme et al. 2018; Paradis et al. 2019). I used phylogenetic least squares (pGLS) regressions to identify statistically significant predictors of gestural repertoire size. The pGLS methods accounts for autocorrelations in the dataset generated by shared ancestry, by including phylogeny as a variance-covariance matrix in the error structure of a least squares regression models (Felsestein 1985; Harvey & Pagel 1991; Harvey & Purvis 1991; Rohlf 2001; Housworth, Martins & Lynch 2004). The phylogeny for this study was derived from the ultrametric molecular tree of mammals in Bininda-Emonds et al (2007), and pruned to include only the species included in the dataset. branch length transformations. Branch lengths were scaled according to Pagel’s lambda set to maximum likelihood (Freckleton, Harvey & Pagel 2002), which was selected as the transformation best fitting to the dataset after graphical comparisons with delta and kappa estimators (using the profile.pgls function in caper; Orme et al. 2018).

Gestural repertoire size was entered as the dependent variable in multivariate pGLS models. Explanatory variables included predictors: breeding groups size, male mating strategy, degree of sympatry, habitat openness, and research effort. Body mass and breeding group size were log-transformed prior to analyses, in order to meet the assumptions of residual normality and homoscedasticity (graphically checked using the plot.pgls function in the package caper; Orme et al. 2018). Model simplification was implemented via progressive removal of non-significant predictors, in order of least significance ($p \leq 0.05$; Murthaugh 2014). The results presented here pertain to the final model including only significant predictors: statistics for non-significant predictors were obtained by separately adding each of them to the final model. Variance inflation factors (VIFs) were calculated to estimate multicollinearity between independent variables. All VIFs were ≤ 2.04, and thus well below the commonly accepted threshold of concern (5-10; McClave & Sincich 2003).

2.3 RESULTS

The repertoire of gestural courtship displays in male bovids and cervids was significantly predicted by breeding group size, male mating strategy, degree of sympatry, and male body mass in multivariate analyses ($F_{5,88} = 11.43$; $P < 0.0001$; $\lambda = 0.41$; $R^2 = 0.36$; **Table 2**). According to the expectations of the Sexual Selection hypothesis, repertoire size was positively correlated with breeding group size (**Table 2**; **Figure 1**). Moreover, repertoires were significantly larger in species adopting non-territorial and lek mating strategies, rather than resource-based territoriality (in both univariate and bivariate models; **Table 2**; **Table 3**). In line with the predictions of the Species Recognition hypothesis, gestural repertoire size was also positively associated with the degree of sympatry with heterospecifics (**Table 2**; **Figure 2**). Male body mass had a negative impact on gestural repertoires: larger species presented less elaborate displays than smaller species (**Table 2**; **Figure 3**), consistent with the proposition that size-based constraints are more severe in the former. Both degree of sympatry and male body mass only emerged as significant predictors of repertoire size in multivariate models, after controlling for the indicators of the intensity of sexual selection (**Table 3**). No effects of habitat openness (**Table 2**; **Figure 4**) and research efforts (**Table 2**; **Figure 5**) could be detected, neither in bivariate nor in multivariate analyses.

2.4 DISCUSSION

I found that the complexity of gestural courtship displays in male bovids and cervids was primarily under sexual selection. Specifically, the size of gestural repertoires appeared to be positively correlated with large breeding groups, and with both non-territorial and lek mating strategies – all indicative of strong sexual selection on males. The comparative analyses simultaneously pointed to species recognition as a driver of complexity, since bovids and cervids living in sympatry with multiple heterospecifics also presented larger gestural repertoires. Furthermore, larger species presented smaller repertoires, revealing the possible presence of constraints imposed by body mass on movement-based displays.

The majority of bovids and cervids adopting resource-based territoriality scored very low (< 5) for gestural repertoires, likely due to the smaller potential for male polygyny associated with this mating strategy (Bro-Jørgensen 2007; Plard, Bonenfant & Gaillard 2011; Bowyer et al. 2020). On the other hand, the large repertoires attained by several species with dominance-mediated access to reproduction (e.g. reindeer *Rangifer tarandus*, Himalayan tahr *Hemitragus jemlahicus*, wild goats *Capra* spp.) suggest that gestural display complexity represents a key target of sexual selection in non-territorial systems (Owen-Smith 1977; Jarman 1983). Although non-territoriality might impose restrictions on the expression of female preferences (due to dominant individuals monopolizing copulations; Bro-Jørgensen 2007, 2011; Clutton-Brock & McAuliffe 2009), evidence exists that females in dominance-based societies actively avoid mating with subordinate males (e.g. bighorn sheep *Ovis canadensis*; Geist 1971; Hogg 1987, 1988; American bison *Bison bison* Berger & Cunningham 1991, 1994; Bowyer et al. 2007; moose *Alces alces* Bowyer et al. 2011). The elaborate courtship displays of non-territorial ungulates might thus provide cues to male rank as a crucial determinant of female mate choice (Jarman 1983; Clutton-Brock, Albon & Guinness 1986; Pelletier & Festa-Bianchet 2006), whereas female choice in territorial species may rather be based on territorial quality (Bro-Jørgensen 2011; Bowyer et al. 2020).

Lek-breeding bovids and cervids presented larger gestural repertoires than species defending resource-based territories. These patterns confirm my expectations that the disproportionate skew in male mating success associated with lek territoriality constitutes a powerful engine for the evolution of courtship display complexity (cf. displays in lekking birds of paradise; Miles & Fuxjager 2018b). Since leks facilitate the assessment of multiple males by visiting oestrous females (Balmford, Albon & Blakeman 1992; Bro-Jørgensen

2002, 2008), my findings also suggest that gestural displays play a role in affecting the outcome of mate choice (as observed in birds: e.g. Andersson 1989; Gibson, Bradbury & Vehrencamp 1991). However, previous studies have found mating preferences of female ungulates on leks to be largely dictated by territory location (e.g. central versus peripheral; Balmford, Rosser & Albon 1992; Bro-Jørgensen 2002; Bro-Jørgensen & Durant 2003), and there is therefore a scope for future studies to look at the interactions between territorial, phenotypic, and behavioural male traits in determining mating success on leks.

The effects of the degree of sympatry on gestural repertoire size was significant only after controlling for breeding group size and male mating strategy, which explained a greater amount of interspecific variation. Courtship displays in bovids and cervids with analogous mating systems tended to be more complex in those species overlapping in distribution with several closely-related heterospecifics. For example, the wild goat (*Capra aegagrus*) and markhor (*Capra falconeri*) of the species-rich Himalayan region (Schaller 1977), exhibited larger gestural repertoires than the Alpine ibex (*Capra ibex*), which does not occur in sympatry with other members of the same tribe (despite equal or smaller breeding group size in the former; Appendix II). Similar patterns were observed in various monogamous antelopes (e.g. duikers of the genus *Cephalophus*; Appendix II). Co-existing with several heterospecifics thus appeared to promote further elaboration of sexually-selected courtship displays, by favouring the addition of new components.

The results corroborate the hypothesis that complexity in gestural courtship displays has evolved as a pre-copulatory barrier against hybridization. Behavioural mechanisms of reproductive isolation are of crucial importance to bovids and cervids, which cannot innately identify conspecifics – to the point of developing mating preferences for other species in cross-fostering experiments (Walther 1991; Kendrick et al. 2001). Larger gestural repertoires might offer a greater opportunity for display divergence among closely-related species (as proposed for other taxa; e.g. Miles et al. 2017; Johnson 2000; Ota 2020), and thus improve the ability of females to recognize conspecific males during courtship (cf. Wagner, Pavlicev & Cheverud 2007; Freeberg et al. 2012). Substantiating these claims, pairing trials show that small gestural repertoires are ineffective at averting hybridization: female red brocket deer (*Mazama* spp.; repertoire size ≤ 3), readily accept copulations with heterospecific males (Carranza, Roldan & Duarte 2018). Now it is necessary to understand whether the opposite is also true, that higher levels of courtship display complexity can prevent interspecific mating.

The negative correlations between gestural display complexity and male body mass demand further exploration. Movement requires higher energetic expenditures in large-bodied mammals (Blanckenhorn 2000), and could thus impose severe costs on the ability to perform elaborate gestural displays. Moreover, large ungulates also frequently sport exaggerated cranial weapons and neck appendages (Geist 1966; Bro-Jørgensen 2016), which likely constitute additional impediments to fine-scale gestures during courtship (cf. the very small repertoires of bovines and moose, all characterized by long horns/antlers and dewlaps; Estes 1991). I therefore suggest that physiological and morphological disadvantages might have concurred to limit gestural display complexity in very large species.

2.5 CONCLUSION

This study provides comparative evidence that the complexity of gestural courtship displays in male bovids and cervids is promoted by sexual selection, and by the degree of sympatry with closely-related species. My findings thus indicate that, in addition to male mating competition, the risk of hybridization connected with sympatric distribution might also constitute a key driver of elaborate displays. Field research is now needed to determine whether gestural complexity might effectively serve a species recognition function during courtship in ungulates and other taxonomic groups.

2.6 TABLES

Table 1: Hypotheses on the evolution of complex gestural courtship displays in male bovids and cervids. Symbols in cells refer to the expected correlation between gestural repertoire size, and selected independent variables (0 = no correlation; + = positive correlation; - = negative correlation).

	Predictors of gestural repertoire size			
Hypotheses	Group size	Mating strategy	Degree of sympatry	Habitat openness
Sexual selection	+	+ Lek + Non-Territorial	0	0
Species recognition	0	0	+	0
Signal efficacy	0	0	0	-

Table 2: PGLS correlations between the repertoire size of gestural courtship displays in male bovids and cervids, and various socio-ecological traits. Coefficients estimates and statistical significance are provided for a multivariate model containing all significant predictors ($F_{5,88}$ = 11.43; λ= 0.412; p = <0.001; R^2 = 0.359).

	B	S.E.	t	P
Mating Strategy - *Lek*	3.170	0.734	4.320	<0.001
Mating Strategy – *Non-territorial*	2.381	0.482	4.944	<0.001
Group Size (log)	0.703	0.209	3.364	0.001
Body Mass (log)	-0.601	0.210	-2.864	0.001
Degree of Sympatry	0.190	0.065	2.922	0.005
Habitat Openness	-0.132	1.129	-0.117	0.907
Research Effort	0.001	0.001	1.048	0.298

Table 3: PGLS correlations between gestural repertoire size and various socio-ecological variables in bivariate models, with only one predictor entered at a time.

	B	S.E.	t	P
Mating Strategy - *Lek*	2.980	0.774	3.851	<0.001
Mating Strategy – *Non-territorial*	2.079	0.458	4.541	<0.001
Group Size (log)	0.634	0.205	3.100	0.003
Body Mass (log)	0.141	0.224	0.632	0.529
Degree of Sympatry	0.099	0.078	1.273	0.206
Habitat Openness	1.441	1.154	1.249	0.215
Research Effort	0.001	0.001	1.415	0.160

2.7 FIGURES

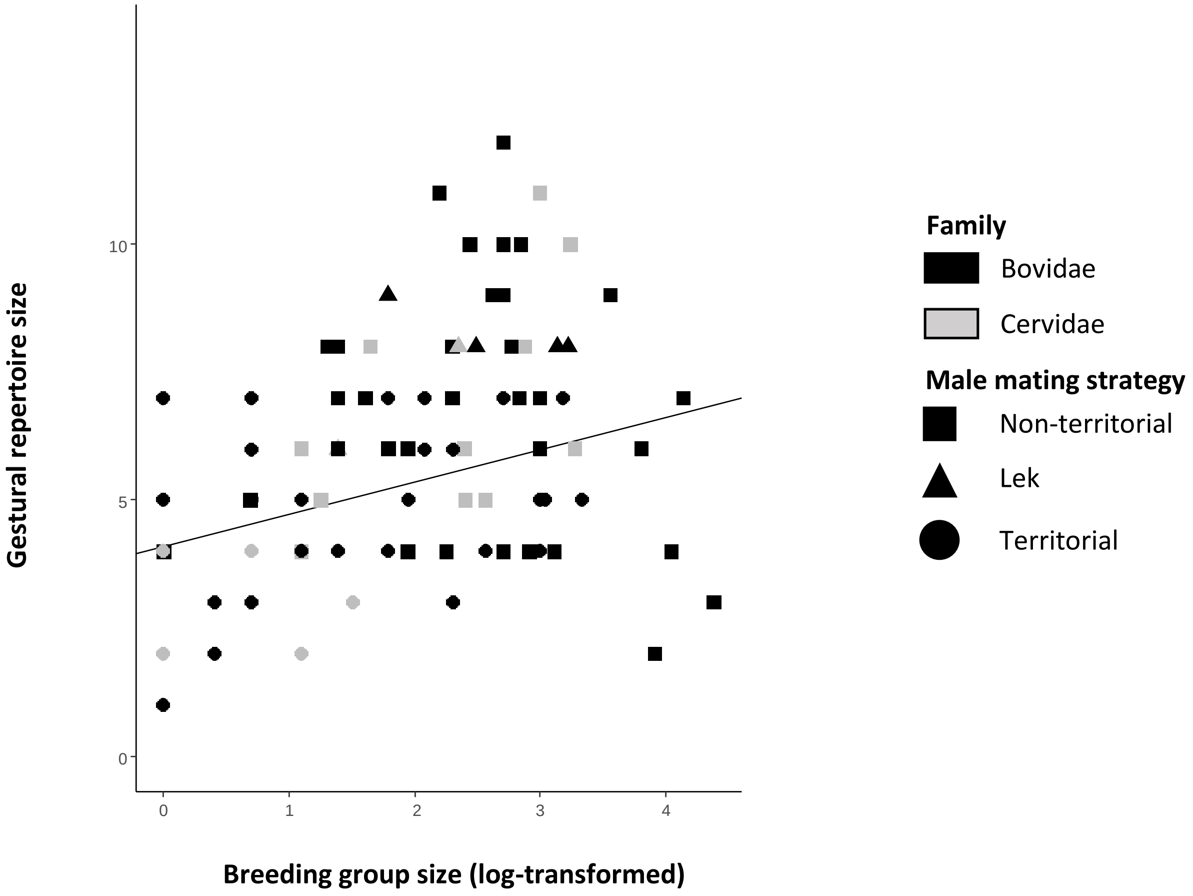


Fig. 1: Gestural complexity of courtship displays in male bovids and cervids plotted against breeding group size (log-transformed). Data are not corrected for phylogeny. The slope and intercept of the regression line were obtained using the Phylogenetic Least Square method.

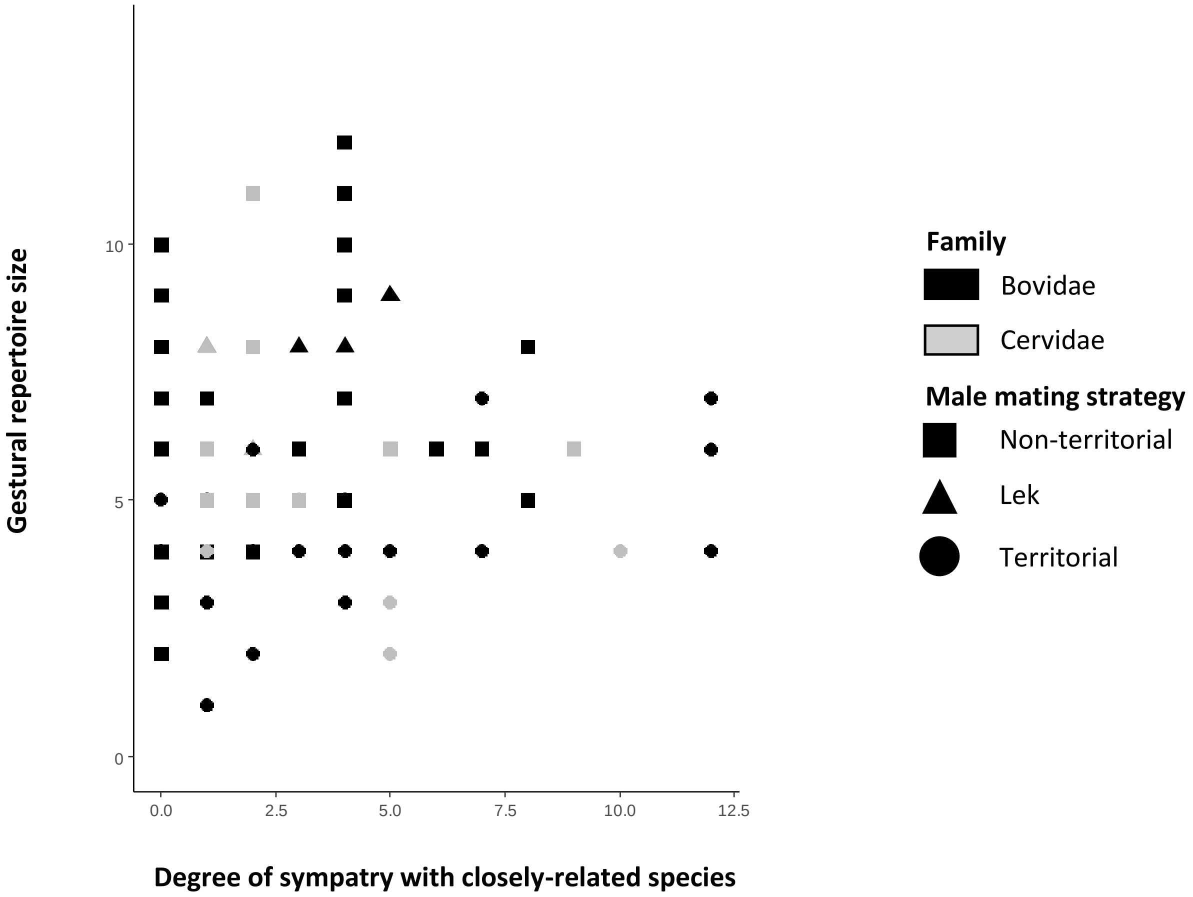


Fig. 2: Gestural complexity of courtship displays in male bovids and cervids, plotted against degree of sympatry (i.e. the number of sympatric heterospecifics in the same tribe). Data are not corrected for phylogeny.

Fig. 3: Gestural complexity of courtship displays in male bovids and cervids, plotted against male body mass (log-transformed). Data are not corrected for phylogeny.

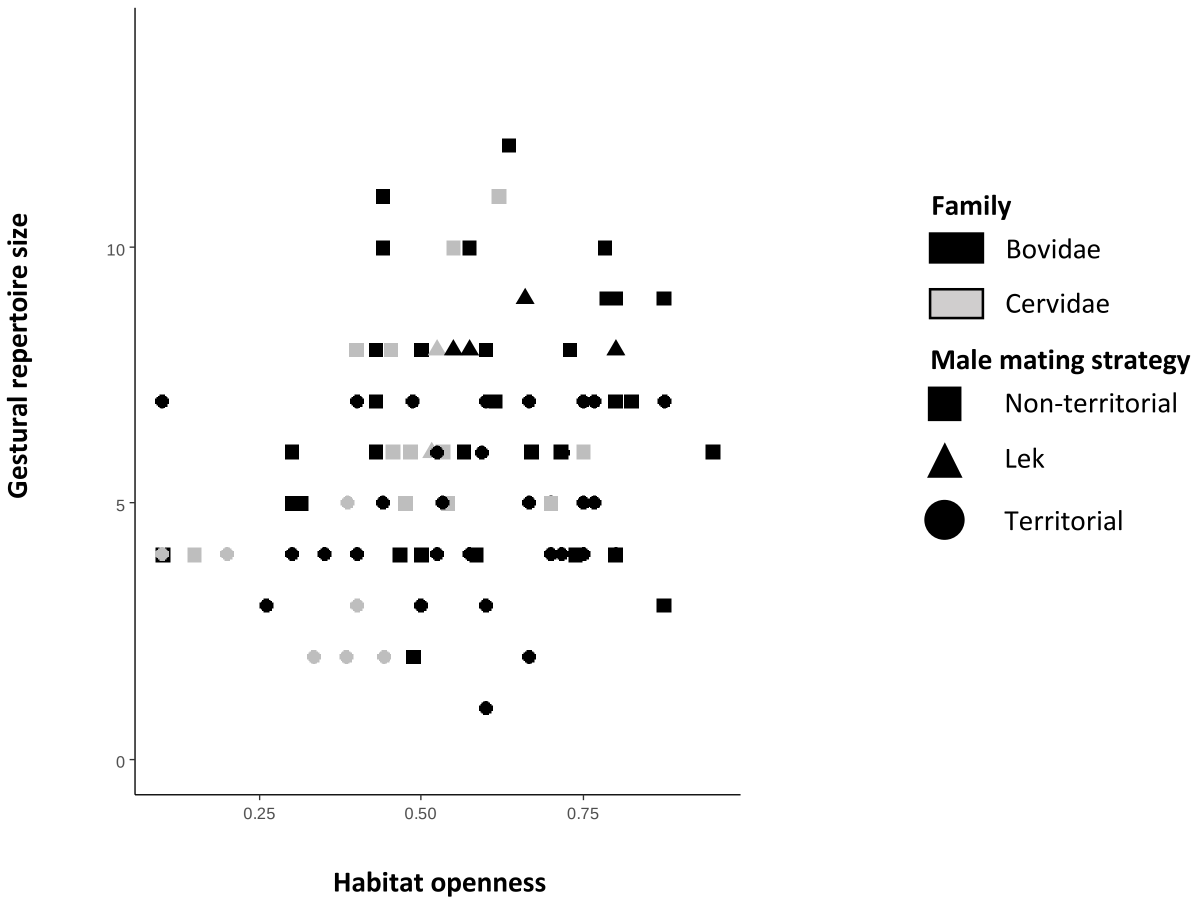


Fig. 4: Gestural complexity of courtship displays in male bovids and cervids, plotted against habitat openness calculated for each study species as scores assigned to IUCN habitat categories. Data are not corrected for phylogeny.

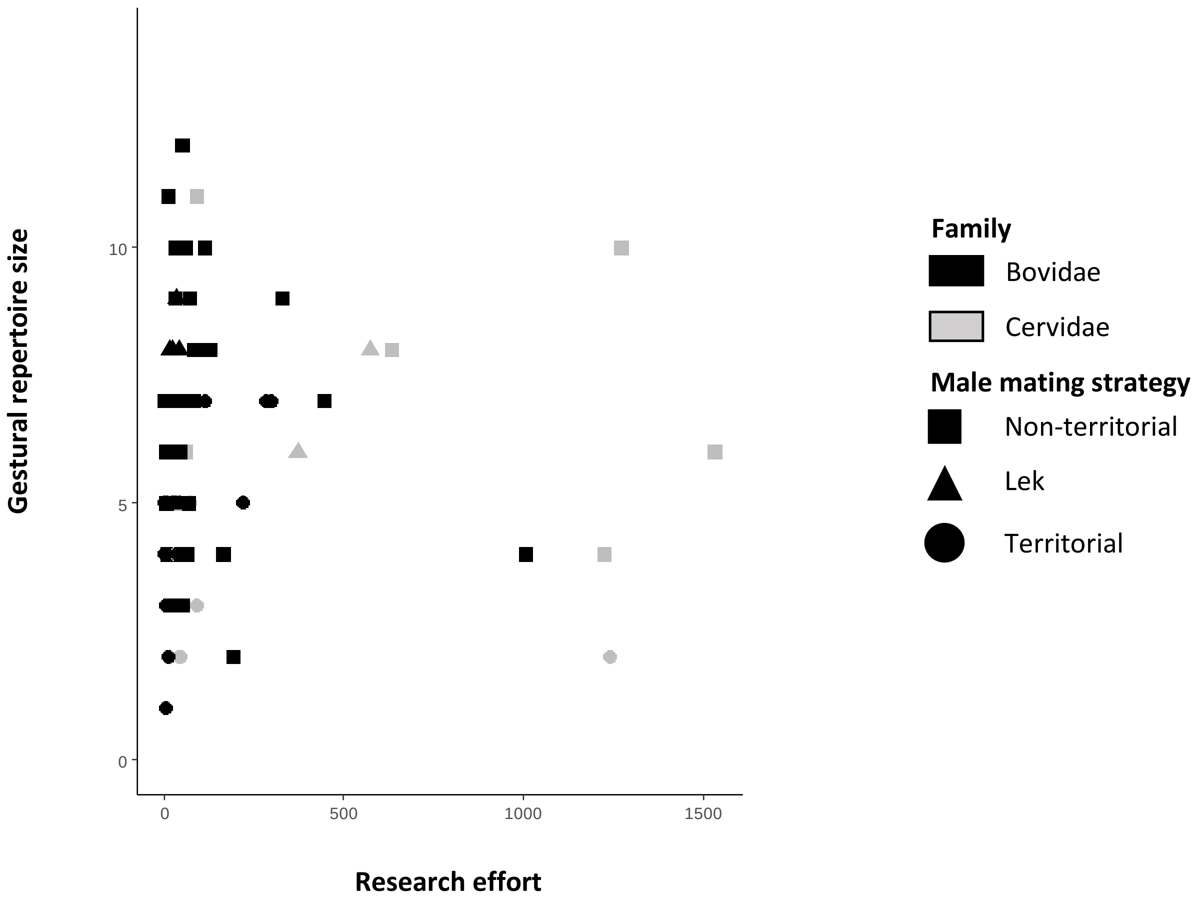


Fig. 5: Gestural complexity of courtship displays in male bovids and cervids, plotted against research effort, intended as the number of citations for each study species from ISI Web of Knowledge. Data are not corrected for phylogeny.

2.8 REFERENCES

Andersson, S. (1989). Sexual selection and cues for female choice in leks of Jackson's widowbird Euplectes jacksoni. *Behavioral Ecology and Sociobiology*, **25**(6), 403-410.

Amo, L., & Bonadonna, F. (2018). The importance of olfaction in intra-and interspecific communication. *Frontiers in Ecology and Evolution*, **6**, 71.

Andersson, M. (1994). *Sexual selection* (Vol. 72). Princeton University Press.

Apollonio, M., Festa-Bianchet, M., Mari, F., Mattioli, S., & Sarno, B. (1992). To lek or not to lek: mating strategies of male fallow deer. *Behavioral Ecology*, **3**(1), 25-31.

Balmford, A., Albon, S., & Blakeman, S. (1992). Correlates of male mating success and female choice in a lek-breeding antelope. *Behavioral Ecology*, **3**(2), 112-123.

Balmford, A., Rosser, A. M., & Albon, S. D. (1992). Correlates of female choice in resource-defending antelope. *Behavioral Ecology and Sociobiology*, **31**(2), 107-114.

Barske, J., Schlinger, B. A., Wikelski, M., & Fusani, L. (2011). Female choice for male motor skills. *Proceedings of the Royal Society B: Biological Sciences*, 278(1724), 3523-3528.

Berger, J., & Cunningham, C. (1991). Bellows, copulations, and sexual selection in bison (*Bison bison*). *Behavioral Ecology*, **2**(1), 1-6.

Berger, J., & Cunningham, C. (1994). *Bison: mating and conservation in small populations*. Columbia University Press.

Bininda-Emonds, O. R., Cardillo, M., Jones, K. E., MacPhee, R. D., Beck, R. M., Grenyer, R., & Purvis, A. (2007). The delayed rise of present-day mammals. *Nature*, **446**(7135), 507-512.

Bowyer, R. T., Bleich, V. C., Manteca, X., Whiting, J. C., & Stewart, K. M. (2007). Sociality, mate choice, and timing of mating in American bison *(Bison bison*): effects of large males. *Ethology*, **113**(11), 1048-1060.

Bowyer, R. T., Rachlow, J. L., Stewart, K. M., & Van Ballenberghe, V. (2011). Vocalizations by Alaskan moose: female incitation of male aggression. *Behavioral Ecology and Sociobiology*, **65**(12), 2251-2260.

Bowyer, R. T., McCullough, D. R., Rachlow, J. L., Ciuti, S., & Whiting, J. C. (2020). Evolution of ungulate mating systems: Integrating social and environmental factors. *Ecology and Evolution*. In press.

Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication*. Sinauer.

Bro-Jørgensen, J. (2002). Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences*, **99**(14), 9290-9293.

Bro-Jørgensen, J. (2007). The intensity of sexual selection predicts weapon size in male bovids. *Evolution*, **61**(6), 1316-1326.

Bro-Jørgensen, J. (2008). The impact of lekking on the spatial variation in payoffs to resource-defending topi bulls, Damaliscus lunatus. *Animal Behaviour*, **75**(4), 1229-1234.

Bro-Jørgensen, J. (2010). Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends in Ecology & Evolution*, **25**(5), 292-300.

Bro-Jørgensen, J. (2011). Intra-and intersexual conflicts and cooperation in the evolution of mating strategies: lessons learnt from ungulates. *Evolutionary Biology*, **38**(1), 28-41.

Bro-Jørgensen, J. (2016). Evolution of the ungulate dewlap: thermoregulation rather than sexual selection or predator deterrence?. *Frontiers in Zoology*, **13**(1), 1-7.

Bro-Jørgensen, J., & Durant, S. M. (2003). Mating strategies of topi bulls: getting in the centre of attention. *Animal Behaviour*, *65*(3), 585-594.

Byers, J., Hebets, E., & Podos, J. (2010). Female mate choice based upon male motor performance. *Animal Behaviour*, **79**(4), 771-778.

Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews*, **78**(4), 575-595.

Carranza, J., Roldán, M., & Duarte, J. M. B. (2018). Lack of mate selectivity for genetic compatibility within the red brocket deer *Mazama americana* complex. *Mammalian Biology*, **88**(1), 168-175.

Cassini, M. H. (2020). Sexual size dimorphism and sexual selection in artiodactyls. *Behavioral Ecology*. In Press.

Chen, I. P., Stuart-Fox, D., Hugall, A. F., & Symonds, M. R. (2012). Sexual selection and the evolution of complex color patterns in dragon lizards. *Evolution*, **66**(11), 3605-3614.

Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proceedings of the Royal Society of London. B. Biological Sciences*, **236**(1285), 339-372.

Clutton-Brock, T. (2016). *Mammal societies*. John Wiley & Sons.

Clutton-Brock, T. (2017). Reproductive competition and sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **372**(1729), 20160310.

Clutton-Brock, T. H., Deutsch, J. C., & Nefdt, R. J. C. (1993). The evolution of ungulate leks. *Animal Behaviour*, **46**(6), 1121-1138.

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1986). Great expectations: dominance, breeding success and offspring sex ratios in red deer. *Animal Behaviour*, **34**(2), 460-471.

Clutton-Brock, T., & McAuliffe, B. K. (2009). Female mate choice in mammals. *The Quarterly Review of Biology*, **84**(1), 3-27.

Coombes, H. A., Stockley, P., & Hurst, J. L. (2018). Female chemical signalling underlying reproduction in mammals. *Journal of chemical ecology*, **44**(9), 851-873.

Dalziell, A. H., Peters, R. A., Cockburn, A., Dorland, A. D., Maisey, A. C., & Magrath, R. D. (2013). Dance choreography is coordinated with song repertoire in a complex avian display. *Current Biology*, **23**(12), 1132-1135.

Darwin, C. (1871). *The descent of man, and selection in relation to sex*. John Murray, London.

Doucet, S. M., Mennill, D. J., & Hill, G. E. (2007). The evolution of signal design in manakin plumage ornaments. *The American Naturalist*, **169**(S1), S62-S80.

Douglas, K. C., Halbert, N. D., Kolenda, C., Childers, C., Hunter, D. L., & Derr, J. N. (2011). Complete mitochondrial DNA sequence analysis of Bison bison and bison–cattle hybrids: Function and phylogeny. *Mitochondrion*, **11**(1), 166-175.

Dunn, J. C., & Smaers, J. B. (2018). Neural correlates of vocal repertoire in primates. *Frontiers in Neuroscience*, **12**, 534.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**(4300), 215-223.

Estes, R. D. (1991). *The behaviour guide to African mammals: including hoofed mammals, carnivores, primates*. Russell Friedman Books CC, Johannesburg.

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, **125**(1), 1-15..

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**(6), 712-726.

Freeberg, T. M., Dunbar, R. I., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 1785-1801.

Fusani, L., Giordano, M., Day, L. B., & Schlinger, B. A. (2007). High-speed video analysis reveals individual variability in the courtship displays of male golden-collared manakins. *Ethology*, **113**(10), 964-972.

Fusani, L., Barske, J., Day, L. D., Fuxjager, M. J., & Schlinger, B. A. (2014). Physiological control of elaborate male courtship: female choice for neuromuscular systems. *Neuroscience & Biobehavioral Reviews*, **46**, 534-546.

Fuxjager, M. J., & Schlinger, B. A. (2015). Perspectives on the evolution of animal dancing: a case study of manakins. *Current Opinion in Behavioral Sciences*, **6**, 7-12.

Fuxjager, M. J., Eaton, J., Lindsay, W. R., Salwiczek, L. H., Rensel, M. A., Barske, J., & Schlinger, B. A. (2015). Evolutionary patterns of adaptive acrobatics and physical performance predict expression profiles of androgen receptor–but not oestrogen receptor–in the forelimb musculature. *Functional Ecology*, **29**(9), 1197-1208.

Fuxjager, M. J., Miles, M. C., Goller, F., Petersen, J., & Yancey, J. (2017). Androgens support male acrobatic courtship behavior by enhancing muscle speed and easing the severity of its tradeoff with force. *Endocrinology*, **158**(11), 4038-4046.

Geist, V. (1966). The evolution of horn-like organs. *Behaviour*, **27**(2), 175-214.

Geist, V. (1971). *Mountain sheep. A study in behavior and evolution*. University of Chicago Press.

Gibson, R. M., Bradbury, J. W., & Vehrencamp, S. L. (1991). Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. *Behavioral Ecology*, **2**(2), 165-180.

Grant, P. R., & Grant, B. R. (1997). Hybridization, sexual imprinting, and mate choice. *The American Naturalist*, **149**(1), 1-28.

Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology* (Vol. 239). Oxford: Oxford university press.

Harvey, P. H., & Purvis, A. (1991). Comparative methods for explaining adaptations. *Nature*, **351**(6328), 619-624.

Heindl, M., & Winkler, H. (2003). Vertical lek placement of forest-dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. *Biological Journal of the Linnean Society*, **80**(4), 647-658.

Hill, G. E. (2015). Sexiness, individual condition, and species identity: the information signaled by ornaments and assessed by choosing females. *Evolutionary Biology*, **42**(3), 251-259.

Hogg, J. T. (1987). Intrasexual competition and mate choice in Rocky Mountain bighorn sheep. *Ethology*, **75**(2), 119-144.

Hogg, J. T. (1988). Copulatory tactics in relation to sperm competition in Rocky Mountain bighorn sheep. *Behavioral Ecology and Sociobiology*, **22**(1), 49-59.

Höglund, J., & Alatalo, R. V. (1995). *Leks*. Princeton University Press.

Hoskin, C. J., & Higgie, M. (2010). Speciation via species interactions: the divergence of mating traits within species. *Ecology Letters*, **13**(4), 409-420.

Housworth, E. A., Martins, E. P., & Lynch, M. (2004). The phylogenetic mixed model. *The American Naturalist*, **163**(1), 84-96.

Isvaran, K. (2005). Variation in male mating behaviour within ungulate populations: patterns and processes. *Current Science*, 1192-1199.

Isvaran, K., & Jhala, Y. (2000). Variation in lekking costs in blackbuck (Antilope cervicapra): relationship to lek-territory location and female mating patterns. *Behaviour*, **137**(5), 547-563.

Jarman, P. (1983). Mating system and sexual dimorphism in large terrestrial, mammalian herbivores. *Biological Reviews*, **58**(4), 485-520.

Johnson, K. P. (2000). The evolution of courtship display repertoire size in the dabbling ducks (Anatini). *Journal of Evolutionary Biology*, **13**(4), 634-644.

Jorge, W., Butler, S., & Benirschke, K. (1976). Studies on a male eland× kudu hybrid. *Reproduction*, **46**(1), 13-16.

Kendrick, K. M., Hinton, M. R., Atkins, K., Haupt, M. A., & Skinner, J. D. (1998). Mothers determine sexual preferences. *Nature*, **395**(6699), 229-230.

Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. *Evolution*, *36*(1), 1-12.

Kirkpatrick, M. (1987). Sexual selection by female choice in polygynous animals. *Annual Review of Ecology and Systematics*, **18**(1), 43-70.

Kozak, E. C., & Uetz, G. W. (2016). Cross-modal integration of multimodal courtship signals in a wolf spider. *Animal Cognition*, **19**(6), 1173-1181.

Leuthold, W. (1977). *African ungulates: a comparative review of their ethology and behavioral ecology* (Vol. 8). Springer Science & Business Media.

Ligon, R. A., Diaz, C. D., Morano, J. L., Troscianko, J., Stevens, M., Moskeland, A., ... & Scholes III, E. (2018). Evolution of correlated complexity in the radically different courtship signals of birds-of-paradise. *PLoS Biology*, **16**(11).

Lorenz, K. (1953). *Comparative studies on the behaviour of Anatinae*. Read Books Ltd.

Lorenz, K. Z. (1958). The evolution of behavior. *Scientific American*, **199**(6), 67-82.

Lorenz, K. 1971. Comparative studies of the motor patterns of Anatinae. In R. Martin (ed.), *Studies in Animal and Human Behaviour*, **2**, 14–114. Methuen, London, UK.

Lüpold, S., Simmons, L. W., & Grueter, C. C. (2019). Sexual ornaments but not weapons trade off against testes size in primates. *Proceedings of the Royal Society B*, **286**(1900), 20182542.

McClave, J. T., & Sincich, T. (2013). *Statistics*. Pearson Education.

McComb, K., & Clutton-Brock, T. H. (1994). Is mate choice copying or aggregation responsible for skewed distributions of females on leks? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **255**(1342), 13-19.

Miles, M. C., Cheng, S., & Fuxjager, M. J. (2017). Biogeography predicts macro-evolutionary patterning of gestural display complexity in a passerine family. *Evolution*, **71**(5), 1406-1416.

Miles, M. C., & Fuxjager, M. J. (2018a). Animal choreography of song and dance: a case study in the montezuma oropendola, *Psarocolius montezuma*. *Animal Behaviour*, **140**, 99-107.

Miles, M. C., & Fuxjager, M. J. (2018b). Synergistic selection regimens drive the evolution of display complexity in birds of paradise. *Journal of Animal Ecology*, **87**(4), 1149-1159.

Miles, M. C., Goller, F., & Fuxjager, M. J. (2018). Physiological constraint on acrobatic courtship behavior underlies rapid sympatric speciation in bearded manakins. *Elife*, **7**, e40630.

Mitoyen, C., Quigley, C., & Fusani, L. (2019). Evolution and function of multimodal courtship displays. *Ethology*, **125**(8), 503-515.

Moller, A. P., & Pomiankowski, A. (1993). Why have birds got multiple sexual ornaments?. *Behavioral Ecology and Sociobiology*, **32**(3), 167-176.

Muniz, D. G., & Machado, G. (2018). Mate sampling influences the intensity of sexual selection and the evolution of costly sexual ornaments. *Journal of Theoretical Biology*, **447**, 74-83.

Munoz, N. E., & Blumstein, D. T. (2012). Multisensory perception in uncertain environments. *Behavioral Ecology*, **23**(3), 457-462.

Murtaugh, P. A. (2014). In defense of P values. *Ecology*, **95**(3), 611-617.

Ord, T. J., Blumstein, D. T., & Evans, C. S. (2001). Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**(1468), 737-744.

Ord, T. J., Blumstein, D. T., & Evans, C. S. (2002). Ecology and signal evolution in lizards. *Biological Journal of the Linnean Society*, **77**(1), 127-148.

Ord, T. J., & Stuart-Fox, D. (2006). Ornament evolution in dragon lizards: multiple gains and widespread losses reveal a complex history of evolutionary change. *Journal of Evolutionary Biology*, **19**(3), 797-808.

Ord, T. J., & Stamps, J. A. (2008). Alert signals enhance animal communication in “noisy” environments. *Proceedings of the National Academy of Sciences*, **105**(48), 18830-18835.

Ord, T. J., & Stamps, J. A. (2009). Species identity cues in animal communication. *The American Naturalist*, **174**(4), 585-593.

Ord, T. J., King, L., & Young, A. R. (2011). Contrasting theory with the empirical data of species recognition. *Evolution*, **65**(9), 2572-2591.

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., & Fritz, S. (2018). The caper package: comparative analysis of phylogenetics and evolution in R. *R package version*, **5**(2), 1-36.

Ota, N., Gahr, M., & Soma, M. (2015). Tap dancing birds: the multimodal mutual courtship display of males and females in a socially monogamous songbird. *Scientific Reports*, **5**(1), 1-6.

Ota, N. (2020). Tap dancers in the wild: field observations of multimodal courtship displays in socially monogamous songbirds. *The Science of Nature*, **107**(4), 1-5

Owen-Smith, N. (1977). On territoriality in ungulates and an evolutionary model. *The Quarterly Review of Biology*, **52**(1), 1-38.

Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claude, J., Cuong, H. S., & Desper, R. (2019). Package ‘ape’. *Analyses of Phylogenetics and Evolution,* **2**(4).

Partan, S. R. (2013). Ten unanswered questions in multimodal communication. *Behavioral Ecology and Sociobiology*, **67**(9), 1523-1539.

Partan, S. R. (2017). Multimodal shifts in noise: switching channels to communicate through rapid environmental change. *Animal Behaviour*, **124**, 325-337.

Pelletier, F., & Festa-Bianchet, M. (2006). Sexual selection and social rank in bighorn rams. *Animal Behaviour*, **71**(3), 649-655.

Plard, F., Bonenfant, C., & Gaillard, J. M. (2011). Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver. *Oikos*, **120**(4), 601-606.

QGIS Development Team (2019). QGIS Geographic Information System. Open Source Geospatial Foundation Project. URL: http://qqgis.osgeo.org/.

R Development Core Team (2019). A language environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Robinson, T. J., Cernohorska, H., Schulze, E., & Duran-Puig, A. (2015). Molecular cytogenetics of tragelaphine and alcelaphine interspecies hybrids: hybridization, introgression and speciation in some African antelope. *Biology Letters*, **11**(11), 20150707.

Rohlf, F. J. (2001). Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution*, **55**(11), 2143-2160.

Rosenthal, G. G. (2013). Individual mating decisions and hybridization. *Journal of Evolutionary Biology*, **26**(2), 252-255.

Santana, S. E., Lynch Alfaro, J., & Alfaro, M. E. (2012). Adaptive evolution of facial colour patterns in Neotropical primates. *Proceedings of the Royal Society B: Biological Sciences*, **279**(1736), 2204-2211.

Santana, S. E., Alfaro, J. L., Noonan, A., & Alfaro, M. E. (2013). Adaptive response to sociality and ecology drives the diversification of facial colour patterns in catarrhines. *Nature Communications*, **4**(1), 1-7.

Schaller, G. B. (1977). *Mountain monarchs. Wild sheep and goats of the Himalaya*. University of Chicago Press.

Schaller, G. B. (2000). *Wildlife of the Tibetan steppe*. University of Chicago Press.

Scholes, E., & Laman, T. G. (2018). Distinctive courtship phenotype of the Vogelkop Superb Bird-of-Paradise *Lophorina niedda* Mayr, 1930 confirms new species status. *Peerj*, **6**, e4621

Shuster, S. M., & Wade, M. J. (2003). *Mating systems and strategies* (Vol. 61). Princeton University Press.

Stankowich, T., & Campbell, L. A. (2016). Living in the danger zone: exposure to predators and the evolution of spines and body armor in mammals. *Evolution*, **70**(7), 1501-1511.

Taylor, C. R., Heglund, N. C., & Maloiy, G. M. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology*, **97**(1), 1-21.

Taylor, R. C., & Ryan, M. J. (2013). Interactions of multisensory components perceptually rescue túngara frog mating signals. *Science*, **341**(6143), 273-274.

Tinbergen, N. (1954a). The courtship of animals. *Scientific American*, **191**(5), 42-47.

Tinbergen, N. (1954b). *The origin and evolution of courtship and threat display*. In Huxley, A. C. Hardy and E. B. Fords (Eds.) *Evolution as a Process*, 233-249.

Vaz Pinto, P., Beja, P., Ferrand, N., & Godinho, R. (2016). Hybridization following population collapse in a critically endangered antelope. *Scientific Reports*, **6**, 18788.

Vrba, E. S., & Schaller, G. B. (2000). Phylogeny of Bovidae based on behavior, glands, skulls, and postcrania. In Vrba, E.S., & Schaller, G. B. (Eds.). *Antelopes, Deer and Relatives*. Yale University Press, New Haven and London.

Wade, M. J., & Arnold, S. J. (1980). The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. *Animal Behaviour*, **28**(2), 446-461.

Wade, M. J., & Shuster, S. M. (2004). Sexual selection: harem size and the variance in male reproductive success. *The American Naturalist*, **164**(4), 83-89.

Wagner, G. P., Pavlicev, M., & Cheverud, J. M. (2007). The road to modularity. *Nature Reviews Genetics*, **8**(12), 921-931.

Walther, F. R. (1974). Some reflections on expressive behaviour in combats and courtship of certain horned ungulates.

Walther, F. R. (1984). *Communication and expression in hoofed mammals*. Indiana University Press.

Walther, F. R. (1991). On herding behavior. *Applied Animal Behaviour Science*, **29**(1-4), 5-13.

Wong, B. B., Candolin, U., & Lindström, K. (2007). Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *The American Naturalist*, **170**(2), 184-189.

Zahavi, A. (1975). Mate selection—a selection for a handicap. *Journal of Theoretical Biology*, **53**(1), 205-214.

2.9 APPENDIX I

List of gestural displays

Head and neck

Low-stretch: the neck and head are held parallel, with the neck stretched forward associated with slight rising of the chin. Head and neck are parallel to the main horizontal body axis. Modifiers of the low-stretch include head nodding or jerking. *Synonyms*: head-low, over-stretch, neck-stretch.

Head down: the neck and head are aligned and point towards the ground, form a diagonal line in respect to the body horizontal axis in a lateral view. The head down can include a jerking movement, with head and neck suddenly raised, with a rapid vertical or sub-vertical movement.

Head-turn: from an alert/proud position, the head is turned away from the receiver (female or opponent), with the muzzle pointing in the opposite direction and oriented either towards the left or towards the right shoulder of the sender. The head and neck can also be moved from side to side (e.g. from normal standing position towards left shoulder, back to central position, and towards the right shoulder), along a sub-horizontal axis, in a rapid head-flagging sequence. *Synonyms*: head flagging, averted gaze, looking away, head orienting.

Nose-up: the neck and head are lifted and held pointing towards the sky. Head nodding or jerking can act as visual modifiers of the nose-up posture. *Synonyms*: nose-lifting, head-up.

Head twisting: with a stretched forward neck position, the head is rotated vertically along the neck axis, with the dorsal head surface oriented either towards the left shoulder or towards the right shoulder, and cranial weaponry pointing away from the intended receiver.

Swan-neck: the chin is retracted towards the ventral surface of the raised neck (maintained in a proud posture), resulting in a frontal exposure of horns or antlers. Swan-neck posture might include a tactile component when the male pushes the female with the base or the tip of the horns. *Synonyms*: horn presentation, chin-tucking.

Tongue flicking: the tongue is protruded and retracted from the mouth, in a sequence of quick flashing movements, or in a prolonged protrusion. *Synonyms*: empty licking.

Empty biting: exaggerated jaw snapping, similar to a true biting action. . Sometimes it is combined with a chewing motion Ritualized mouth opening (i.e. with no immediate mechanical function) and exposure of the lower incisors through retraction of the lips were also conservatively lumped under this display category. Tooth baring during Flehmen responses, as probably constituting a mere executive behaviour, was not included in the display complexity score. *Synonyms*: snapping.

1. Front legs

Foreleg kick: a single foreleg is lifted from standing position and extended towards the female, and may or not may not touch the female abdomen (or other ventral areas), depending on the stage of the courtship display (contact is usually observed just prior to attempted or successful mounting). Stiff and flexed kicking (where the carpal joint is flexed during the action) were combined here as they might be homologous gestural elements (Schaller 1977), and as they do not occur together in the same species (thus not affecting the final scoring of display complexity), except perhaps for bharal (*Pseudois nayaur*; Schaller 1977). *Synonyms*: front kick, foreleg lifting.

Kneeling or squatting: dropping down on the anterior carpal joints or on elbow joints.

Flank stroke: slowly caressing or poking female rump or flank with a lifted front leg (the leg might be lifted to the point that the carpal joint is at shoulder level or higher). The front leg is flexed at the carpal joint, slightly rotated so that the inner surface of the leg or of the hoof is in contact with the female flank. *Synonyms*: croup touch.

Pawing: digging in the soil with one front hoof.

2. Hind legs only

Hunching: both hind legs are retracted under the abdomen from a normal standing position, resulting into hunching of the back and lowering of the rump towards the ground.

Cavorting: hind legs are thrown into the air in a rapid motion.

3. Front and hind legs

Bipedalism: rising on the hind legs. Forelegs usually move in a pattern often described as “empty kicking”; however, not enough details are provided in available literature sources to determine the actual occurrence of this gestural element as an independent display motor pattern.

High-lift gait: exaggerated rising and lowering of both front legs and hind legs, at a slow pace. Different authors defined exaggerated gaits in different species as “prancing”, “stiff walk”, or “style-trotting”, because of species-specific variations in the visual motor output of the gait. However, most available descriptions do not provide enough details in order to differentiate between the different styles of high-lifting gaits. Furthermore, only one form of exaggerated gait is included in sexual displays in each of the species considered for this study, and thus the lumping of various behavioural categories did not affect the final complexity score. *Synonyms*: prancing, stiff walk, style-trotting.

Crouching: all four legs are bent in an exaggeratedly low posture, with belly almost touching the ground. Movements of the legs are stiff and possibly akin to those observed in prancing. It is restricted to only two bovid and one cervid species.

4. Tail

Tail erection: the tail is moved away from its usual resting position. Here horizontal tail erection and vertical tail erection were combined together, as data from literature was not always sufficient to discriminate between these two motor patterns. Furthermore, both horizontal and vertical tail erection might co-occur within a species, simply as expression of different levels of male excitation (Walther 1984). Lateral movements of the tail, often termed as “flicking” or “slashing”, were also lumped under “tail movements”, as descriptions of tail gestures often did not provide enough information to distinguish between simple erection and other actions. *Synonyms*: tail erection, tail flagging, tail flicking, tail curling, tail exposure, tail slashing.

5. Combined display elements

Neck fight: the male pushes downwards with the ventral part of its neck against the dorsal surface of the female neck. The neck-head posture is similar to that adopted for low-stretch. The orientation of the male in respect to the female varies from frontal to parallel.

Chin-resting: the male lays the ventral part of the muzzle on the dorsal part of the female rump. Neck and head are stretched horizontally.

Erectile display: the penis is unsheathed and ejaculation might occur. The unsheathing occurring just prior to mounting was not considered as an element of sexual display, but rather as a mechanical gesture, and thus not included in the complexity scoring. *Synonyms*: penis unsheathed, penis display.

Urine spraying: urine is sprayed from erected and unsheathed penis, targeting the flow towards different regions of the body (targeted regions are species-specific). This gestural element might be accompanied by other body movements aimed at intercepting the urine flow, which were however considered as mechanical actions and not as display elements (detailed information on the single motor patterns included in the process is also currently unavailable).

2.10 APPENDIX II

Dataset

Species	Gestural Display Complexity	Group size	Habitat Openness	Male Body Mass (Kg)	Research Effort	Degree of Sympatry	Mating Strategy
Bovidae							
Addax nasomaculatus	6	20	0.95	117.7	17	1	NT
Aepyceros melampus	5	20	0.75	56.9	221	0	T
Alcelaphus buselaphus	3	10	0.6	178.3	26	4	T
Ammotragus lervia	6	3	0.715784	111.8	48	1	NT
Antidorcas marsupialis	7	24	0.766667	40.7	81	0	T
Antilope cervicapra	8	23	0.8	40.2	24	1	L
Bison bison	4	57	0.584615	795.3	1007	0	NT
Bos frontalis	4	9.5	0.1	848.4	65	1	NT
Bos grunniens	3	80	0.875	590.5	53	0	NT
Boselaphus tragocamelus	4	7	0.466667	253.3	24	1	NT
Bubalus quarlesi	4	1	0.1	150	11	1	NT
Budorcas taxicolor	4	22.5	0.5	282.7	24	0	NT
Capra falconeri	11	9	0.44	92.7	12	4	NT
Capra hircus	12	15	0.635714	53	52	4	NT
Capra ibex	9	15	0.8	80.5	329	0	NT
Capra nubiana	7	20	0.825	70	37	1	NT
Capra pyrenaica	8	10	0.5	72.5	129	0	NT
Capra sibirica	9	13.8	0.7875	90	32	4	NT
Cephalophus monticola	7	2	0.1	4.4	59	12	T
Cephalophus rufilatus	7	1	0.4	10.1	8	12	T
Cephalophus silvicultor	4	2	0.35	52.5	6	12	T
Cephalophus zebra	4	1	0.1	13.9	3	7	T
Connochaetes gnou	5	21	0.7	166.7	23	4	T
Connochaetes taurinus	7	15	0.766667	235.3	115	4	T
Damaliscus lunatus	9	6	0.66	137	35	5	L
Damaliscus pygargus	7	8	0.666667	71.1	44	4	T
Gazella dama	4	6	0.716667	68	40	1	T
Gazella dorcas	7	17	0.75	16.3	74	7	T
Gazella gazella	7	6	0.875	23.3	286	0	T
Gazella granti	6	10	0.72	72.1	18	2	T
Gazella soemmerringii	5	7	0.666667	45.4	4	4	T
Gazella subgutturosa	7	4	0.8	27.4	55	4	NT
Gazella thomsonii	5	28	0.75	22.7	9	1	T
Hemitragus hylocrius	6	7	0.67	100	9	0	NT
Hemitragus jemlahicus	10	15	0.44	103.3	32	4	NT
Hippotragus equinus	4	13	0.525	274.4	32	3	T
Hippotragus niger	4	20	0.4	235.2	57	2	T
Kobus ellipsiprymnus	6	8	0.525	236.8	42	7	T
Kobus kob	8	25	0.575	97.5	45	4	L
Kobus leche	8	12	0.55	104.3	16	3	L
Litocranius walleri	4	3	0.7	35	9	5	T
Madoqua kirkii	3	2	0,5	4.6	8	1	T
Madoqua saltiana	4	2	0.3	2.3	3	2	T

Naemorhedus baileyi	5	2	0.44	25.6	3	4	T
Naemorhedus crispus	5	1	0.53333	35.9	42	0	T
Naemorhedus goral	7	8	0.4875	32	10	1	T
Neotragus moschatus	3	1.5	0.26	4.8	6	0	T
Oreamnos americanus	8	4	0.6	95.9	111	0	NT
Oryx gazella	4	18.5	0.7375	210	49	2	NT
Ourebia ourebi	5	3	0.766667	14.1	31	0	T
Ovibos moschatus	4	15	0.8	356	165	0	NT
Ovis canadensis	7	10	0.8	83.4	447	0	NT
Ovis dalli	8	3.7	0.73	80.4	89	0	NT
Ovis vignei	7	63	0.614286	50	82	4	NT
Pantholops hodgsonii	7	17	0.8	42.3	17	0	NT
Pelea capreolus	4	4	0.75	24	6	0	T
Pseudois nayaur	10	11.5	0.783333	60	61	4	NT
Raphicerus campestris	2	1.5	0.666667	10.9	14	2	T
Raphicerus melanotis	1	1	0.6	10.7	6	1	T
Redunca arundinum	4	3	0.575	58.3	6	4	T
Redunca redunca	4	4	0.8	51.6	34	5	T
Rupicapra pyrenaica	10	17.2	0.575	34	115	0	NT
Rupicapra rupicapra	7	20	0.6	40.3	298	0	T
Saiga tatarica	9	35	0.875	42.5	73	0	NT
Sylvicapra grimmia	6	2	0.594444	18.3	34	12	T
Syncerus caffer	2	50	0.4875	642.9	193	0	NT
Taurotragus oryx	6	45	0.566667	647.3	47	7	NT
Tragelaphus angasii	6	4	0.43	110.2	7	3	NT
Tragelaphus eurycerus	6	6	0.3	300	20	6	NT
Tragelaphus imberbis	7	5	0.43	95.6	4	4	NT
Tragelaphus scriptus	5	2	0.3	49.7	70	8	NT
Tragelaphus spekii	5	2	0.314286	102.3	8	4	NT
Tragelaphus strepsiceros	8	16	0.43	240.8	84	8	NT
Cervidae							
Alces alces	4	3	0.15	482.5	1226	0	NT
Axis axis	11	20	0.62	75	93	2	NT
Axis porcinus	6	11	0.48333	42.7	19	3	NT
Capreolus capreolus	2	3	0.33333	25	1241	0	T
Capreolus pygargus	2	3	0.383333	43.8	48	1	T
Cervus albirostris	6	26.5	0.533333	204.2	10	1	NT
Cervus duvaucelii	5	13	0.475	234	10	3	NT
Cervus elaphus	8	17.7	0.4	350	107	2	NT
Cervus nippon	6	4	0.516667	122	373	2	L
Cervus unicolor	3	4.5	0.4	234	94	5	T
Dama dama	8	10.5	0.525	70	574	1	L
Hippocamelus antisensis	5	11.05	0.7	60	7	2	NT
Hippocamelus bisulcus	5	3.5	0.540909	95	40	1	NT
Mazama americana	4	1	0.1	29	52	10	T
Mazama gouazoupira	2	1	0.442857	18	42	5	T
Muntiacus reevesi	5	2	0.385714	8.5	75	3	T
Odocoileus hemionus	8	5.2	0.452857	86	634	2	NT
Odocoileus virginianus	6	3	0.455882	71.5	1533	9	NT

Ozotoceros bezoarticus	6	4	0.75	40	61	5	NT
Pudu puda	4	2	0.2	13.5	32	1	T
Rangifer tarandus	10	25.5	0.55	250	1274	0	NT

References for gestural courtship display complexity

Alados, C. L. (1984). Etograma de la cabra montés (*Capra pyrenaica*) y comparación con otras especies. *Donana Acta Vertebrata*, **11**, 289-309.

Alados, C. L. (1986). Aggressive behaviour, sexual strategies and their relation to age in male Spanish ibex (*Capra pyrenica*). *Behavioural Processes*, **12**(2), 145-158.

Anderson, J. L. (1980). The social organisation and aspects of behaviour of the nyala *Tragelaphus angasi* Gray, 1849. *Zeitschrift für Säugetierkunde*, **19** (45), 141-152.

Annighöfer, P., & Schütz, S. (2011). Observations on the population structure and behaviour of two differently managed populations of the greater kudu (*Tragelaphus strepsiceros*, Pallas 1766) in Namibia. *European Journal of Wildlife Research*, **57**(4), 895-907.

Ballenberghe, V. V., & Miquelle, D. G. (1993). Mating in moose: timing, behavior, and male access patterns. *Canadian Journal of Zoology*, **71**(8), 1687-1690.

Barrette, C. (1977). The social behaviour of captive muntjacs *Muntiacus reevesi* (Ogilby 1839). *Zeitschrift für Tierpsychologie*, **43**(2), 188-213.

Barrio, J. (2013). Hippocamelus antisensis. *Mammalian Species*, **45**(901), 49-59.

Berg, J. K. (1987). Behaviour of the Japanese serow (*Capricornis crispus*) at the San Diego Wild Animal Park. In Soma, H. (ed). *The Biology and Management of Capricornis and Related Mountain Antelopes*, 165-181. Springer, Dordrecht.

Berger, J., & Cunningham, C. (1994). *Bison: mating and conservation in small populations*. Columbia University Press.

Bigalke, R. C. (1972). Observations on the behaviour and feeding habits of the springbok, *Antidorcas marsupialis*. *African Zoology*, **7**(1), 333-359.

Blank, D. A. (1998). Mating behavior of the Persian gazelle *Gazella subgutturosa* Güldenstaedt, 1780. *Mammalia*, **62**(4), 499-520.

Blank, D., Ruckstuhl, K. E., & Yang, W. (2012). Social organization in goitered gazelle (*Gazella subgutturosa* Güldenstaedt 1780). *Ethology Ecology & Evolution*, **24**(4), 306-321.

Bowyer, T. R., Ballenberghe, V. V., & Kie, J. G. (2003). Moose (*Alces alces*). In Feldhamer, G. A., Thompson, B. C., & Chapman, J. A. (eds). *Wildlife Mammals of North America: Biology, Management, and Consservation, Second Edition*, 931-964. The Johns Hopkins University.

Buechner, H. K., & Schloeth, R. (1965). Ceremonial mating behavior in Uganda kob (*Adenota kob thomasi* Neumann). *Zeitschrift für Tierpsychologie*, **22**(2), 209-225.

Braza, F., Garcia, J. E., & Alvarez, F. (1986). Rutting behaviour of fallow deer. *Acta Theriologica*, **31**(34), 467-478.

Buzzard, P. J., Xu, D., & Li, H. (2014). Sexual/aggressive behavior of wild yak (*Bos mutus* Prejevalsky 1883) during the rut: influence of female choice. *Chinese Science Bulletin*, **59**(22), 2756-2763.

Carranza, J., Roldán, M., Peroni, E. D. F. C., & Duarte, J. M. B. (2017). Weak premating isolation between two parapatric brocket deer species. *Mammalian Biology-Zeitschrift für Säugetierkunde*, **87**, 17-26.

Carranza, J., Roldán, M., & Duarte, J. M. B. (2018). Lack of mate selectivity for genetic compatibility within the red brocket deer *Mazama americana* complex. *Mammalian Biology*, **88**, 168-175.

Chapman, D., & Chapman, N. (1975). *Fallow deer: their history, distribution, and biology*. Dalton.

Corlatti, L., Caroli, M., Pietrocini, V., & Lovari, S. (2013). Rutting behaviour of territorial and nonterritorial male chamois: Is there a home advantage? *BehaviouralPprocesses*, **92**, 118-124.

Danilkin, A. A. (1996). *Behavioural ecology of Siberian and European roe deer*. Chapman & Hall.

David, J. H. M. (1973). The behaviour of the bontebok, *Damaliscus dorcas dorcas*, (Pallas 1766), with special reference to territorial behaviour. *Zeitschrift für Tierpsychologie*, **33**(1), 38-107.Press.

David, J. H. M. (1975). Observations on mating behaviour, parturition, suckling and the mother-young bond in the Bontebok (*Damaliscus dorcas dorcas*). *Journal of Zoology*, **177**(2), 203-223.

David, J. H. M. (1978). Observations on territorial behaviour of springbok, *Antidorcas marsupialis*, in the Bontebok National Park, Swellendam. *African Zoology*, **13**(1), 123-141.

Díaz, N. I., & Smith-Flueck, J. (2001). The Patagonian huemul: a mysterious deer on the brink of extinction. *Mountain Research and Development*, **21**(3).

Dresser, B. L., Romo, J. S., Brownscheidle, C. M., & Russell, P. T. (1980). Reproductive behaviour and birth of a bongo *Boocercus eurycerus* at the Cincinnati Zoo. *International Zoo Yearbook*, **20**(1), 229-234.

Dubost, G. (1980). L 'écologie et la vie sociale du Céphalophe bleu (*Cephalophus monticola* Thunberg), petit ruminant forestier africain. *Zeitschrift für Tierpsychologie*, **54**(3), 205-266.

Dubost, G., & Feer, F. (1988). Variabilité comportementale à l'intérieur du genre *Cephalophus* (Ruminantia, Bovidae), par l'exemple de *C. rufilatus* Gray, 1846. *Zeitschrift für Säugetierkunde*, **53**(1), 31-47.

Espmark, Y. (1964). Rutting behaviour in reindeer (*Rangifer tarandus* L.). *Animal Behaviour*, **12**(1), 159-163.

Estes, R. D. (1967). The comparative behavior of Grants and Thomson's gazelles. *Journal of Mammalogy*, **48**(2), 189-209.

Estes, R. D. (1969). Territorial Behavior of the Wildebeest (*Connochaetes taurinus* Burchell, 1823). *Zeitschrift für Tierpsychologie*, **26**(3), 284-370.

Estes, R. D. (1991). *The behaviour guide to African mammals: including hoofed mammals, carnivores, primates*. Russell Friedman Books CC, Johannesburg.

Estes, R. D., & Estes, R. K. (1974). The biology and conservation of the giant sable antelope, *Hippotragus niger variani* Thomas, 1916. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **126**. 73-104.

Fedosenko, A. K., & Blank, D. A. (2001). Capra sibirica. *Mammalian species*, **675**, 1-13.

Feer, F. (1994). Ethological observations on *Bubalus quarlesi* Ouwens, 1910 in captivity. *Zeitschrift fuer Saeugetierkunde*, **59**(3), 139-152.

Feer, F., & Dubost, G. (1981). The behavior of the male *Antilope cervicapra* L., its development according to age and social rank. *Behaviour*, **76**(1-2), 62-125.

Frädrich, H. (1964). Beobachtungen zur Kreuzung zwischen Schwarzrückenducker*, Cephalophus dorsalis* Gray, 1846, und Zebraducker, *Cephalophus zebra* Gray, 1838. *Zeitschrift für Säugetierkunde*, **29**, 46-51.

Geist, V. (1963). On the behaviour of the North American moose (*Alces alces andersoni* Peterson 1950) in British Columbia. *Behaviour*, **20**(3), 377-415.

Geist, V. (1965). On the rutting behavior of the mountain goat. *Journal of Mammalogy*, **45**(4), 551-568.

Geist, V. (1971). *Mountain sheep. A study in behavior and evolution*. University of Chicago Press.

Geist, V. (1981). Behavior: adaptive strategies in mule deer. In Wallmo, O. C. (ed). *Mule and black-tailed deer of North America,* 157-223. *University of Nebraska Press, Lincoln, USA*.

Geist, V. (1982). Adaptive behavioral strategies. In Thomas, J. W., & Toweill, D. E., (Eds). *Elk of North America: ecology and management*). Stackpole Books.

Geist, V. (1991). Bones of contention revisited: did antlers enlarge with sexual selection as a consequence of neonatal security strategies? *Applied Animal Behaviour Science*, **29**(4), 453-469.

Geist, V. (1998). *Deer of the world: their evolution, behaviour, and ecology*. Stackpole Books.

Gosling, L. M. (1974). The social behaviour of Coke's hartebeest. In Geist, V., & Walther, F. R. (eds). *The behaviour of ungulates and its relation to management,* 1, 488-511. IUCN, Morges, Switzerland.

Grau, G. A., & Walther, F. R. (1976). Mountain gazelle agonistic behaviour. *Animal Behaviour*, **24**(3), 626-636.

Gray, D. R. (1987). *The muskoxen of Polar Bear Pass*. Fitzhenry & Whiteside, Markham, Ontario.

Gray, G. G., & Simpson, C. D. (1980). Ammotragus lervia. *Mammalian Species*, 1-7.

Grobler, J.H. (1974). Aspects of the biology, population ecology and behaviour of the sable antelope *Hippotragus niger niger*, (Harris, 1838) in the Rhode Matopos National Park, Rhodesia. *Arnoldia,* **7**, 1–36.

Habibi, K. (1987). Behavior of aoudad (*Ammotragus lervia*) during the rutting season. *Mammalia*, **51**(4), 497-514.

Habibi, K. (1994). *The desert ibex: life history, ecology and behaviour of the Nubian ibex in Saudi Arabia*. National Commission for Wildlife Conservation and Development (NCWCD).

Habibi, K. (1997). Social behavior of the sand and mountain gazelle. In Habibi, K., Abuzinada, A. H., & Nader, A. I. (eds). *The gazelles of Arabia.* National Commission for Wildlife Conservation and Development (NCWCD).

Habibi, K., Thouless, C. R., & Lindsay, N. (1993). Comparative behaviour of sand and mountain gazelles. *Journal of Zoology*, **229**(1), 41-53.

Jarman, M. V. (1979). *Impala social behaviour: territory, hierarchy, mating, and the use of space*. Parey.

Jewell, P. A. (1972). Social organisation and movements of topi (*Damaliscus korrigum*) during the rut, at Ishasha, Queen Elizabeth Park, Uganda. *African Zoology*, **7**(1), 233-255.

Johnsingh, A. J. T., & Manjrekar, N. (Eds.). (2015). *Mammals of South Asia*. Universities Press India.

Jungius, H. (1971). The biology and behaviour of the reedbuck (*Redunca arundinum* Boddaert 1785) in the Kruger National Park. Parey, Hamburg und Berlin.

Kang, A. (2004). Behavioral research of the saiga antelope, *Saiga tatarica*, in its main reproductive seasons in a semi-natural condition. Unpublished PhD Thesis*.* College of Life Sciences East China Normal University. Harbin.

Caboń-Raczyńska, K., Krasińska, M., Krasiński, Z. A., & Wójcik, J. M. (1987). Rhythm of daily activity and behavior of European bison in the Białowieża Forest in the period without snow cover. *Acta Theriologica*, **32**(21), 335-372.

Kingdon, J. (1982). *East African mammals (bovids). Vol. 3, part C*. London Academic Press.

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

Kojola, I. (1986). Rutting behaviour in an enclosured group of wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.). *Rangifer*, **6**(2), 173-179.

Krämer, A. (1969). Soziale organisation und sozialverhalten einer gemspopulation (*Rupicapra rupicapra* L.) der Alpen. *Zeitschrift für Tierpsychologie*, **26**(8), 889-964.

Kranz, K. R. (1991). Monogamy in the dik-dik. *Applied Animal Behaviour Science*, **29**(1), 87-105.

Kucera, T. E. (1978). Social behavior and breeding system of the desert mule deer. *Journal of Mammalogy*, **59**(3), 463-476.

Lent, P. C. (1965). Rutting behaviour in a barren-ground caribou population. *Animal Behaviour*, **13**(2-3), 259-264.

Lent, P. C. (1969). A preliminary study of the Okavango lechwe*: Kobus leche leche* Gray. *African Journal of Ecology*, **7**(1), 147-157.

Leslie, D. M. (2008). Boselaphus tragocamelus. *Mammalian Species*, **813**, 1-16.

Leslie Jr, D. M. (2010). Przewalskium albirostre. *Mammalian Species*, **849**, 7-18.

Leuthold, W. (1978). On social organization and behaviour of the gerenuk *Litocranius walleri* (Brooke 1878). *Zeitschrift für Tierpsychologie*, **47**(2), 194-216.

Linsdale, J. M., & Tomich, P. Q. (1953). *A herd of mule deer*. Univesity of California Press.

Lobao-Tello, J. P., & Van Gelder, R. G. (1975). The natural history of nyala, *Tragelaphus angasi* (Mammalia, Bovidae) in Mozambique. *Bullettin of the American Museum of Natural History,* **155**(4), 323-385.

Lott, D. F. (1974). Sexual and aggressive behavior of adult male American bison (*Bison bison*). In Geist, V., and Walther, F. R. (eds). *The behaviour of ungulates and its relation to management*, *1*, 382-394. IUCN, Morges, Switzerland.

Lott, D. F. (1981). Sexual behavior and intersexual strategies in American bison. *Zeitschrift für Tierpsychologie*, *56*(2), 97-114.

Lott, D. F. (2002). *American bison: a natural history* (Vol. 6). University of California Press.

Lovari, S., (1984). *Il popolo delle rocce*. Rizzoli.

Lovari, S. (1985). Behavioural Repertoire of the Abruzzo Chamois*, Rupicapra pyrenaica ornata* Neumann, 1899 (Artiodactyla: Bovidae). *Saugetierkundliche Mitteilungen*, **32**(2), 85.

Lovari, S., & Cosentino, R. (1986). Seasonal habitat selection and group size of the Abruzzo chamois (*Rupicapra pyrenaica ornata*). *Italian Journal of Zoology*, **53**(1), 73-78.

Lovari, S., & Locati, M. (1991). Temporal relationships, transitions and structure of the behavioural repertoire in male Apennine chamois during the rut. *Behaviour*, **119**(1), 77-103.

Lovari, S., & Apollonio, M. (1994). On the rutting behaviour of the Himalayan goral *Nemorhaedus goral* (Hardwicke, 1825). *Journal of Ethology*, **12**(1), 25-34.

Lumpkin, S., & Kranz, K. R. (1984). Cephalophus sylvicultor. *Mammalian Species* **127**, 1-7.

Mainguy, J., & Côté, S. D. (2008). Age-and state-dependent reproductive effort in male mountain goats, *Oreamnos americanus*. *Behavioral Ecology and Sociobiology*, **62**(6), 935-943.

MacNamara, M., & Eldridge, W. (1987). Behavior and reproduction in captive pudu (*Pudu puda*) and red brocket *(Mazama americana*) a descriptive and comparative analysis. In Wemmer, C. M. (ed). *Biology and management of the Cervidae*, 371-386, Research symposia of the National Zoological Park Smithsonian Institution, Washington, D.C.

Manski, D. A. (1991). Reproductive behavior of addax antelope. *Applied Animal Behaviour Science*, **29**(4), 39-66.

Masui, M. (1987). Social behaviour of Japanese serow, *Capricornis crispus crispus*. In Soma, H. (ed). *The Biology and Management of Capricornis and Related Mountain Antelopes*, 134-144. Springer, Dordrecht.

Miura, S. (1984). Social behavior and territoriality in male sika deer (*Cervus nippon* Temminck 1838) during the rut. *Zeitschrift für Tierpsychologie*, **64**(1), 33-73.

Miura, S., Ohtaishi, N., Kaji, K., & Wu, J. (1988). A Preliminary Study of Behavior and Acoustic Repertoire of Captive White-lipped Deer, *Cervus albirostris*, in China. *Journal of the Mammalogical Society of Japan*, **13**(2), 105-118.

Mloszewski, M. J. (1983). *Behavior and ecology of the African buffalo*. Cambridge University Press.

Monfort-Braham, N. (1975). Variations dans la structure sociale du topi, *Damaliscus korrigum* Ogilby, au Pare National de l'Akagera, Rwanda. *Zeitschrift für Tierpsychologie*, **39**(1-5), 332-364.

Morales-Piñeyrúa, J. T., & Ungerfeld, R. (2012). Pampas deer (*Ozotoceros bezoarticus*) courtship and mating behavior. *Acta Veterinaria Scandinavica*, **54**(1), 60.

Mungall, E. C. (1980). Courtship and mating behavior of the Dama gazelle (*Gazella dama* Pallas 1766). *Zoologiche Garten*, **50**, 1-14.

Miller, R. (1975). Notes on the behaviour of hog deer in an enclosure. *Bullettin of the Siam natural History Society*, **26**(1-2), 105-131.

Neas, J. F., & Hoffmann, R. S. (1987). Budorcas taxicolor. *Mammalian Species*, **277**, 1-7.

Nievergelt, B. (1967). Die zusammensetzung der gruppen beim alpensteinbock. *Zeitschrift für Säugetierkunde*, **32**, 129-144.

Novellie, P. A., Manson, J., & Bigalke, R. E. (1984). Behavioural ecology and communication in the Cape grysbok. *African Zoology*, **19**(1), 22-30.

Owen-Smith, N. (1993). Age, size, dominance and reproduction among male kudus: mating enhancement by attrition of rivals. *Behavioral Ecology and Sociobiology*, **32**(3), 177-184.

Pohle, C. (1987). Experiences of keeping and breeding saiga antelope at Tierpark, Berlin. In Soma, H. (ed). *The Biology and Management of Capricornis and Related Mountain Antelopes*, 191-204. Springer, Dordrecht.

Povilitis, A. (1985). Social behavior of the huemul (*Hippocamelus bisulcus*) during the breeding season. *Zeitschrift für Tierpsychologie*, **68**(4), 261-286.

Powell, D., Speeg, B., Li, S., Blumer, E., & McShea, W. (2013). An ethogram and activity budget of captive Sichuan takin (*Budorcas taxicolor tibetana*) with comparisons to other Bovidae. *Mammalia*, **77**(4), 391-401.

Reinhardt, V. (1985). Courtship behavior among musk-ox males kept in confinement. *Zoo Biology*, **4**(3), 295-300.

Rice, C. G. (1988). Agonistic and sexual behavior of Nilgiri tahr (*Hemitragus hylocrius*). *Ethology*, **78**(2), 89-112.

Rice, C. G. (1995). On the origin of sexual displays in caprids. *Zeitschrift für Säugetierkunde*, **60**(1), 53-62.

Schaller, G. B. (1967). *The deer and the tiger*. University of Chicago Press.

Schaller, G. B. (1970). Observations on Nilgiri tahr (*Hemitragus hylocrius* Ogilby, 1838). *Journal of the Bombay Natural History Society*, **67**(3), 365-389.

Schaller, G. B. (1973). Observations on Himalayan tahr (*Hemitragus jemlahicus*). *Journal of the Bombay Natural History Society,* **70**, 1-24.

Schaller, G. B. (1973). On the behaviour of blue sheep (*Pseudois nayaur*). *Journal of the Bombay Natural History Society*, **69**, 523-537.

Schaller, G. B. (1977). *Mountain monarchs. Wild sheep and goats of the Himalaya*. University of Chicago Press.

Schaller, G. B. (2000). *Wildlife of the Tibetan steppe*. University of Chicago Press.

Schaller, G. B., & Laurie, A. (1974). Courtship behaviour of the wild goat. *Zeitschrift für Saugetierkunde*, **39**(2), 115-127.

Schaller, G. B., & Mirza, Z. B. (1971). On the behavior of Kashmir markhor (*Capra falconeri cashmiriensis*). *Mammalia*, **35**(4), 548-566.

Schaller, G. B., & Mirza, Z. B. (1974). On the behaviour of Punjab urial (*Ovis orientalis punjabiensis*). In Geist, V., and Walther, F. R. (eds). *The behaviour of ungulates and its relation to management*, *1*, 306-323. IUCN, Morges, Switzerland.

Schenkel, R. (1966). On sociology and behaviour in impala (*Aepyceros melampus lichtensteini*). *African Journal of Ecology*, **4**(1), 99-114.

Scholte, P., & Hashim, I. M. (2013). *Gazella dorcas* Dorcas *gazelle.* In Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., & Kalina, J. (eds). *Mammals of Africa* (Vol. 6), 340-346. A&C Black.

Schuster, R. H. (1976). Lekking behavior in Kafue lechwe. *Science*, **192**(4245), 1240-1242.

Simonetta, A. M. (1966). Osservazioni etologiche ed ecologiche sui dik-dik (gen. *Madoqua*, Mammalia, Bovidae) in Somalia. *Monitore Zoologico Italiano*, **74**(1), 1-33.

Sinclair, A. R. E. (1977*). The African buffalo; a study of resource limitation of populations*. University of Chicago Press, Chicago, USA.

Skinner, J. D., & Louw, G. N. (1996). *The Springbok: Antidorcas marsupialis (Zimmermann, 1780)*. Transvaal Museum.

Sokolov, V. E. (1974). Saiga tatarica. *Mammalian Species*, **38**, 1-4.

Spinage, C. A. (1969). Naturalistic observations on the reproductive and maternal behaviour of the Uganda defassa waterbuck *Kobus defassa ugandae* Neumann. *Zeitschrift für Tierpsychologie*, **26**(1), 39-47.

Spinage, C. (1982). *A territorial antelope: the Uganda waterbuck*. Elsevier.

Tener, J. S. (1965). *Muskoxen in Canada: a biological and taxonomic review* (Vol. 2). Department of Northern Affairs and National Resources, Canadian Wildlife Service.

Ungerfeld, R., González-Pensado, S., Bielli, A., Villagrán, M., Olazabal, D., & Pérez, W. (2008). Reproductive biology of the pampas deer (*Ozotoceros bezoarticus*): a review. *Acta Veterinaria Scandinavica*, **50**(1), 16.

Vats, R., & Bhardwaj, C. S. (2009). A Study of Reproductive Behaviour of Indian Black Buck (*Antilope cervicapra*) Linn. with Reference to Courtship, Breeding, Fawning and Colouration. *Current World Environment*, **4**(1), 121-125.

Von Richter, W. (1971). Observations on the biology and ecology of the black wildebeest (*Connochaetes gnou*). *South African Journal of Wildlife Research*, **1**(1), 3-16.

Von Richter, W. (1972). Territorial behaviour of the black wildebeest *Connochaetes gnou*. *African Zoology*, **7**(1), 207-231.

de Vos, A., Brokx, P., & Geist, V. (1967). A review of social behavior of the North American cervids during the reproductive period. *American Midland Naturalist*, **77**(2), 390-417.

Walther, F. (1958). Zum Kampf-und Paarungsverhalten einiger Antilopen. *Zeitschrift für Tierpsychologie*, **15**(3), 340-380.

Walther, F. (1962). The mating behaviour of certain horned animals. *International Zoo Yearbook*, **3**(1), 70-77.

Walther, F. R. (1964). Einige Verhaltensbeobachtungen an Thomsongazellen (*Gazella thomsoni* Günther, 1884) im Ngorongoro-Krater. *Zeitschrift für Tierpsychologie*, **21**(7), 871-890.

Walther, F. (1964). Verhaltensstudien an der Gattung *Tragelaphus* de Blainville, 1816 in Gefangenschaft, unter besonderer Berücksichtigung des Sozialverhaltens. *Zeitschrift für Tierpsychologie*, **21**(4), 393-467.

Walther, F. R. (1965). Verhaltensstudien an der Grantgazelle (*Gazella granti* Brooke, 1872) im Ngorongoro-Krater. *Zeitschrift für Tierpsychologie*, **22**(2), 167-208.

Walther, F. R. (1974). Some reflections on expressive behaviour in combats and courtship of certain horned ungulates. In Geist, V., and Walther, F. R. (eds). *The behaviour of ungulates and its relation to management*, *1*, 56-106. IUCN, Morges, Switzerland.

Walther, F. R. (1977). Artiodactyla. In Sebeok, T. A. (ed). *How animals communicate*. Indiana University Press.

Walther, F. R. (1980). Aggressive behaviour of oryx antelope at water-holes in the Etosha National Park. *Madoqua*, **11**(4), 271-302.

Walther, F. R. (1984). *Communication and expression in hoofed mammals*. Indiana University Press.

Walther, F. R. (1991). On herding behavior. *Applied Animal Behaviour Science*, **29**(1-4), 5-13.

Walther, F. R., Mungall, E. C., & Grau, G. A. (1983). *Gazelles and their relatives: a study in territorial behavior*. William Andrew Publishing.

Warren, R. J., Vogelsang, R. W., Kirkpatrick, R. L., & Scanlon, P. F. (1978). Reproductive behaviour of captive white-tailed deer. *Animal Behaviour*, **26**, 179-183.

Williamson, D. T. (1994). Social behaviour and organization of red lechwe in the Linyanti Swamp. *African Journal of Ecology*, **32**(2), 130-141.

Wilson, P. (1984). Aspects of reproductive behaviour of bharal (*Pseudois nayaur*) in Nepal. *Zeitschrift für Säugetierkunde*, **49**(1), 36-42.

Wilson, V. J. (2001). *Duikers of Africa: masters of the African forest floor*. Zimbi books.

Wronski, T., Apio, A., Wanker, R., & Plath, M. (2006). Behavioural repertoire of the bushbuck (*Tragelaphus scriptus*): agonistic interactions, mating behaviour and parent–offspring relations. *Journal of Ethology*, **24**(3), 247-260.

Xie, Y. (2006). Primary observations on rutting behavior of the captive red goral. *Zoo Biology*, **25**(2), 117-123.

Yahner, R. H. (1979). Temporal patterns in male mating behavior of captive Reeve's Muntjac (*Muntiacus reevesi*). *Journal of Mammalogy*, **60**(3), 560-567.

2.11 APPENDIX III

References for body mass, breeding group size, and male mating strategy

Anderson, A. E., & Wallmo, O. C. (1984). Odocoileus hemionus. *Mammalian Species*, **219**, 1-9.

Ballenberghe, V. V., & Miquelle, D. G. (1993). Mating in moose: timing, behavior, and male access patterns. *Canadian Journal of Zoology*, **71**(8), 1687-1690.

Barrio, J. (2013). Hippocamelus antisensis. *Mammalian Species*, *45*(901), 49-59.

Bender, L. C. (1996). Harem sizes and adult sex ratios in elk (*Cervus elaphus*). *American Midland Naturalist*, **136**(1),199-202.

Bowyer, T. R., Ballenberghe, V. V., & Kie, J. G. (2003). Moose (*Alces alces*). In Feldhamer, G. A., Thompson, B. C., & Chapman, J. A. (eds). *Wildlife Mammals of North America: Biology, Management, and Consservation, Second Edition*, 931-964. The Johns Hopkins University.

Bro-Jørgensen, J. (2007). The intensity of sexual selection predicts weapon size in male bovids. *Evolution*, **61**(6), 1316-1326.

Bro-Jørgensen, J. (2008). Dense habitats selecting for small body size: a comparative study on bovids. *Oikos*, **117**(5), 729-737.

Bro-Jørgensen, J. (2014). Will their armaments be their downfall? Large horn size increases extinction risk in bovids. *Animal Conservation*, **17**(1), 80-87.

Chapman, D., & Chapman, N. (1975). *Fallow deer: their history, distribution, and biology*. Dalton.

Clutton-Brock, T. H., Albon, S. D., & Harvey, P. H. (1980). Antlers, body size and breeding group size in the Cervidae. *Nature*, **285**(5766), 565.

Danilkin, A. A. (1995). Capreolus pygargus. *Mammalian Species*, **512**, 1-7.

Danilkin, A. A. (1996). *Behavioural ecology of Siberian and European roe deer*. Chapman & Hall.

Duarte, J. M. B., & González, S. (2010). *Neotropical cervidology*. IUCN/FUNEP, Jaboticabal.

Espmark, Y. (1964). Rutting behaviour in reindeer (*Rangifer tarandus* L.). *Animal Behaviour*, **12**(1), 159-163.

Estes, R. D. (1991). *The behaviour guide to African mammals: including hoofed mammals, carnivores, primates*. Russell Friedman Books CC, Johannesburg.

Frid, A. (1994). Observations on habitat use and social organization of a huemul *Hippocamelus bisulcus* coastal population in Chile. *Biological Conservation*, **67**(1), 13-19.

Geist, V. (1963). On the behaviour of the North American moose (*Alces alces andersoni* Peterson 1950) in British Columbia. *Behaviour*, **20**(3), 377-415

Geist, V. (1998). *Deer of the world: their evolution, behaviour, and ecology*. Stackpole Books.

Johnsingh, A. J. T., & Manjrekar, N. (Eds.). (2015). *Mammals of South Asia*. Universities Press India.

Kingdon, J. (1982). *East African mammals (bovids). Vol. 3, part C*. London Academic Press.

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

Kojola, I. (1986). Rutting behaviour in an enclosured group of wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.). *Rangifer*, **6**(2), 173-179.

Kucera, T. E. (1978). Social behavior and breeding system of the desert mule deer. *Journal of Mammalogy*, **59**(3), 463-476.

Holman, L., & Bro-Jørgensen, J. (2016). Ornament complexity is correlated with sexual selection:(a comment on Raia et al., "Cope's Rule and the Universal Scaling Law of Ornament Complexity"). *The American Naturalist*, **188**(2), 272-275.

Leslie Jr, D. M. (2010). Przewalskium albirostre. *Mammalian Species*, **849**, 7-18.

Leslie Jr, D. M. (2011). Rusa unicolor. *Mammalian Species*, **871**, 1-30.

Lott, D. F. (1981). Sexual behavior and intersexual strategies in American bison. *Zeitschrift für Tierpsychologie*, **56**(2), 97-114.

Lott, D. F. (2002). *American bison: a natural history* (Vol. 6). University of California Press.

Lovari, S., (1984). *Il popolo delle rocce*. Rizzoli.

Miura, S. (1984). Social behavior and territoriality in male sika deer (*Cervus nippon* Temminck 1838) during the rut. *Zeitschrift für Tierpsychologie*, **64**(1), 33-73.

Morales-Piñeyrúa, J. T., & Ungerfeld, R. (2012). Pampas deer (*Ozotoceros bezoarticus*) courtship and mating behavior. *Acta Veterinaria Scandinavica*, **54**(1), 60.

Plard, F., Bonenfant, C., & Gaillard, J. M. (2011). Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver. *Oikos*, **120**(4), 601-606.

Povilitis, A. J. (1983). Social organization and mating strategy of the huemul (*Hippocamelus bisulcus*). *Journal of Mammalogy*, **64**(1), 156-158.

Povilitis, A. (1985). Social behavior of the huemul (*Hippocamelus bisulcus*) during the breeding season. *Zeitschrift für Tierpsychologie*, **68**(4), 261-286.

Rabinowitz, A. (1999). Notes on the rare red goral (*Naemorhedus baileyi*) of north Myanmar. *Mammalia (Paris)*, **63**(1), 119-123.

Schaller, G. B. (1967). *The deer and the tiger*. University of Chicago Press.

Schaller, G. B. (1977). *Mountain monarchs. Wild sheep and goats of the Himalaya*. University of Chicago Press.

Schaller, G. B. (2000). *Wildlife of the Tibetan steppe*. University of Chicago Press.

Sielfeld, W., & Guzmán, J. A. (2011). Distribution, reproduction and grouping patterns in the taruca deer (*Hippocamelus antisensis* D'Orbigny, 1834) in the extreme north of Chile. *Animal Production Science*, **51**(4).

Sempéré, A. J., Sokolov, V. E., & Danilkin, A. A. (1996). Capreolus capreolus. *Mammalian Species*, **538**, 1-9.

Smith, W. P. (1991). Odocoileus virginianus. *Mammalian species*, (388), 1-13.

de Vos, A., Brokx, P., & Geist, V. (1967). A review of social behavior of the North American cervids during the reproductive period. *American Midland Naturalist*, **77**(2), 390-417.

Nowak, R. M., & Walker, E. P. (1999). *Walker's Mammals of the World* (Vol. 1). JHU press.

Whitehead, G. K. (1993). *Whitehead encyclopedia of deer*. Voyageur Press.

CHAPTER 3: LIVING IN MIXED-SEX GROUPS LIMITS SEXUAL SELECTION AS A DRIVER OF SEXUAL DIMORPHISM IN COLORATION AND ORNAMENTS IN BOVIDS

ABSTRACT

Among mammals, bovids provide some of the most striking examples of male morphological ornaments, including sexually dimorphic colourations and pelage structures such as beards and manes. Morphological dimorphism is usually interpreted as the outcome of sexual selection on males for signals of quality and/or competitive ability. However, if sexual selection is such a strong force in nature, the absence of dimorphic traits in several species characterized by intense male sexual competition is puzzling, and points to fitness costs imposed on ornamentation by other selection pressures. I therefore applied the comparative method with phylogenetic controls to identify which factors either promoted or constrained the evolution of dimorphism in coloration and ornaments across bovids.

I found that the degree of dimorphism in coloration and ornaments correlated positively with large breeding group size, an indicator of the intensity of sexual selection, and male non-territoriality, which is also likely to affect the operation of sexual selection. The almost complete absence of dimorphic ornaments in species with territorial mating systems is indicative of weaker male competition over reproductive opportunities, and suggests that sexual selection in territorial bovids might target other traits.

Morphological dimorphism was reduced in species forming mixed-sex herds. This suggests that male ornaments may be disadvantageous in societies consisting of multiple males and females, possibly by increasing individual conspicuousness and exposure to predation and to aggression by conspecifics. The need for social integration into mixed-sex herds thus seemingly constitutes a powerful counter-selection regime to the positive drive exerted by sexual selection towards increasing male ornamentation. By contrast, I found no evidence for the hypothesis that lower visibility in dense habitats would cause an attenuation of dimorphism in coloration or ornaments.

3.1 INTRODUCTION

Understanding the ultimate drivers of sexual dimorphism is a central issue in the study of evolutionary biology (Darwin 1871; Lande 1980; Andersson & Iwasa 1996). Differences between males and females encompass various secondary sexual characters, ranging from body size and weaponry (Weckerly 1998; Perez-Barberia, Gordon & Pagel 2002; Cassini 2020), to extravagant morphological ornaments, such as distinctive male colourations or flamboyant appendages (e.g. in birds: Møller & Pomiankowski 1993; Cooney et al. 2019; in primates: Grueter, Isler & Dixson 2015; Lüpold, Simmons & Grueter 2019). Ever since its original theoretical formulation by Darwin (1871), sexual selection has been invoked as the key force behind the evolution of dimorphic male ornaments (e.g. Badyaev & Hill 2000; Shultz & Burns 2017). However, why is morphological dimorphism absent in a large number of species characterized by intense sexual competition? Among mammals, the Bovidae offer some of the most striking examples of dimorphic ornamentation, including the pied coats of male blackbuck (*Antilope cervicapra*), and Nile lechwe (*Kobus megaceros*), and the beards and manes of wild sheep and goats (Schaller 1977; Caro 2009; Kingdon 2015). Nonetheless, equally striking is the virtual monomorphism of several other members of this family, to the point that the two sexes might be difficult to distinguish for a human observer (e.g. blue wildebeest *Connochaetes taurinus*; southern oryx *Oryx gazella*; Estes 1991a; Caro 2009). In this study, I used the comparative method in order to test multiple hypotheses proposed to explain this extreme interspecific variation in morphological dimorphism across bovids.

Sexual selection theory posits that competition between males for mating rights promotes the evolution of ornaments as signals of genetic quality or competitive ability (*Sexual Selection hypothesis*; Darwin 1871; Lande & Arnold 1985; Andersson & Simmons 2006; McCullough, Miller & Emlen 2016). Morphological dimorphism should thus be particularly accentuated in polygynous breeding systems, where more ornamented males can impair the mating success of competitors by attracting more mates or winning more signalling contests (Clutton-Brock, Albon & Harvey 1980; Jarman 1983; Grueter et al. 2015; Cassini 2020). In bovids, the level of polygyny varies according to the species-specific strategies adopted by males to secure copulations (Bro-Jørgensen 2007, 2011; Vanpé et al. 2008; Shuster 2009). An important distinction is between males defending territories, attractive to females due to their location or resources (territorial strategy); and non-territorial males, directly following and defending oestrous females (non-territorial strategy; Gosling 1986; Isvaran 2005). Territoriality implies a reduction in polygyny, as females usually range over multiple territories, thereby forcing males to effectively share reproductive opportunities with rivals (Gosling 1986; Bro-Jørgensen 2007, 2011). By contrast, access to receptive females in non-territorial systems is controlled by individuals attaining top-ranking status in dominance hierarchies, which monopolize breeding groups by actively excluding subordinates from mating (Gosling 1986; Bro-Jørgensen 2007, 2011). Non-territorial strategies are therefore associated with a greater potential for male polygyny and translate into heightened competition, exerting a stronger drive for male ornamental traits than in territorial systems.

Mating strategies can also affect the evolution of morphological dimorphism by determining which male characters are primarily targeted by sexual selection (Andersson 1994). In territorial ungulates, attributes of territories serve a more important role than male ornamentation in mediating intra- and inter-sexual interactions (Owen-Smith 1977; Jarman 1983; Vanpé et al. 2008, 2009). For example, females usually choose mating partners based on territory location or availability of resources, rather than on male physical attributes (e.g. Clutton-Brock et al. 1988; Balmford, Rosser & Albon 1992; Bro-Jørgensen 2002). Territoriality, by offering a spatial reference to male social and reproductive status (i.e. only competitively superior males can acquire high-quality territories; Owen-Smith 1977; Jarman 1983), might thus relax the need for individual-based ornaments as sexual signals, resulting into an attenuation of dimorphism.

Differences in the intensity of sexual selection and in mating strategies, however, cannot account for why morphological dimorphism failed to evolve in many non-territorial, highly polygynous bovids. Various authors have advanced the alternative idea that the distribution of male ornaments in this lineage reflects the degree of spatio-temporal aggregation between the sexes (Geist 1974; Jarman 1983; Estes 1991b, 2000). Ungulates forming social groups consisting of several males and females tend to be less dimorphic than those living in sexually-segregated societies (*Social Integration hypothesis*; Jarman 1983; Geist & Bayer 1988; Estes 1991a, 2000). These patterns likely reflect unsustainable survival and energetic costs deriving from male visual conspicuousness in mixed-sex herds (Jarman 1983; Geist & Bayer 1988). In particular, ornamented individuals would “stand out in a crowd”, offering an easier target to visually-oriented predators (a phenomenon known as “oddity effect”; Landeau & Terborgh 1986; Estes 1991b). Moreover, distinctive cues to sexual identity - provided by dimorphic ornaments - could also attract disproportionately high levels of aggression by other males, catalysing intra-sexual intolerance and ultimately undermining group cohesion (Geist 1977; Estes 1991a, 2000). Non-ornamented, female-like appearances might conversely discourage aggressive behaviour from dominant or territorial individuals (due to the risk of misdirected attacks on females), favouring the integration of multiple males into mixed-sex social groups (Geist 1968; Geist & Bromley 1978; Main & Coblentz 1990; Estes 1991a, 2000). The selective advantages connected with a reduction in sex-biased predation, and in the frequency of male conflicts, might have thus led to sexual monomorphism in species forming mixed-sex herds.

Habitat characteristics limiting visual communication could also exert selection pressures against morphological dimorphism (*Habitat-Mediated Selection hypothesis*; Stuart-Fox & Ord 2004; Bossu & Near 2015; Price 2017). In terrestrial ecosystems, dense vegetation impedes long-range visibility, and therefore the efficacy of ornaments as sexual signals (Bradbury & Vehrencamp 2011). The elaborate, sharp pelage markings of grassland bovids, in contrast to the generally uniform or disruptive colourations of forest species, suggest that the latter might be less reliant on vision than on other sensory channels (Stoner et al. 2003; Caro & Stankowich 2010). Morphological dimorphism should therefore be more pronounced in open habitats, where visual assessment of mates and/or opponents is facilitated by the absence of structural barriers. Additionally, forest-dwelling ungulates usually employ cryptic antipredator strategies to avoid detection (Estes 1991a; Caro et al. 2004): these could be jeopardized by traits such as bright male colourations, which increase the risk of sensory exploitation by predators (Zuk & Kolluru 1998; Stuart-Fox & Ord 2004; Caro 2005a).

I addressed the validity of the three hypotheses discussed above (Sexual Selection; Social Integration; and Habitat-mediated Selection), by focusing on dimorphism in colour and pelage ornaments (e.g. manes, beards) of bovids. Throughout the study, these two traits were together referred to as “morphological dimorphism” which thus does not include sexual body size dimorphism. Under the Sexual Selection hypothesis, I expected the degree of morphological dimorphism on both traits to co-vary with the potential for male polygyny, and thus to be positively correlated with breeding group size (an indicator of the number of females per mating male; Wade & Shuster 2004) and with male non-territoriality. Conversely, dimorphism was predicted to be rare and of small magnitude in territorial bovids, due to low levels of polygyny, and to sexual selection operating on different male traits (e.g. attributes of territories). According to the Social Integration hypothesis, I expected colour and pelage dimorphism to be correlated negatively with the tendency for aggregation in mixed-sex herds. Finally, I predicted, under the Habitat-Mediated Selection hypothesis, that morphological dimorphism would increase with habitat openness. Hypotheses and predictions are summarized in **Table 1**.

3.2 METHODS

Morphological dimorphism

I collected data on morphological dimorphism in 110 of the recognized 136 bovid species. All data relate to the subspecies for which the most detailed data could be obtained. I focused exclusively on the non-domesticated subspecies (e.g. in *Bos frontalis*, *B. grunniens*, and *Capra hircus*), as domestication could potentially alter adaptive colourations and morphologies.

Morphological dimorphism was visually scored on photographs (all in lateral view) obtained from Costello (2016) and from reputable online sources (www.arkive.com; www.encyclopediaoflife.com; www.ultimateungulate.com). A minimum of two (one male and one female) and a maximum of eight (four males and four females) pictures were selected for each species. I used information provided by the sources to ensure that all images referred to the same subspecies, and to the same season (for boreal species presenting different summer and winter coats).

Colour dimorphism was assessed on eight distinct body regions (Caro & Stankowich 2010): (i) head; (ii) neck; (iii) flank and shoulder/humerus; (iv) rump and femur; (v) upper front leg (elbow and ulna); (vi) lower front leg (podials and metapodials); (vii) upper hind leg (knee and tibia); and (viii) lower hind leg (podials and metapodials). Colouration in bovids cannot be considered independently from the presence of contrasting white or black markings, in the form of distinctive stripes, blotches, or spots, against lighter or darker background hair (Stoner et al. 2003; Caro & Stankowich 2010). In order to account for variation deriving from differences both in hair pigmentation, and in the presence/absence of contrasting markings, I scored dimorphism (for each body region) according to a three-point scale: 0 - no difference; 1 - difference in background colour or contrasting markings (presence of markings in one sex only); 2 - difference in both background colour and contrasting markings. In order to be as objective as possible in the scoring process, I compared background hair to a reference of five colour categories, based on the proportions of eumelanin (brown or grey-black) versus phaeomelanin (yellow-red) pigments of mammalian hair (modified from Caro et al. 2017: Caro, Newell & Stankowich 2018): (i) white (de-pigmented); (ii) phaeomelanin - yellow/red; (iii) eumelanin - brown; (iv) eumelanin – grey; (v) eumelanin - black (**Figure 1**). Background colour was scored as dimorphic if the same body region was assigned to different categories in males and females. I conservatively chose not to evaluate differences in colour intensity (e.g. dark versus light brown) within the established colour categories, given that the variable lighting conditions, hair length, and gland secretions could have altered the perceived intensity (Estes 1991a; Caro 2005b; Caro et al. 2017). Dimorphism in contrasting markings was only considered as occurring when distinctive, hard-edged white or black patches (stripes, spots, etc.) were present in one sex and absent in the other (I did not take into account differences in patch size, due to the impossibility of obtaining such measures from non-calibrated pictures). The sum of the scores across all eight body regions was considered as the overall degree of colour dimorphism for each species (Caro et al. 2017).

Following Estes (2000), I considered the followng pelage ornaments: (i) frontal hair tuft; (ii) beard or ventral mane; (iii) dorsal mane; (iv) cape (covering both dorsal and ventral parts of the neck); (v) front leg pantaloons; and (vi) hind leg pantaloons. Pelage dimorphism was scored on a four-point visual scale: 0 - no difference; 1 – the ornament is larger or of different colour in one sex; 2 – the ornament is both larger and of different colour in one sex; 3 – the ornament is present only in one sex. This scale reflected a progression from null to maximum dimorphism (Grueter et al. 2015). The sum of scores for each pelage ornament was considered as the species-specific score of pelage dimorphism.

A second observer, blind to the study hypotheses, double-scored all dimorphism for all bovid species included in this study, using the same methodology: the two independent scores were very similar and highly correlated (Kendall's T = 0.978; $p < 0.0001$). This confirmed the repeatability of my approach, despite the fact that a certain degree of subjectivity could not be avoided.

Independent variables

Data on average breeding group size and male mating strategy was derived from literature sources listed in the Appendix. Male mating strategy was classified as a binary character: territorial (T), or non-territorial (NT). Lek breeding is observed in only four bovid species, and always co-exists with resource-defending territorial strategies (Clutton-Brock, Deutsch & Nefdt 1993): due to the very small sample size (unsuitable for statistical analyses) it was therefore lumped with territoriality.

The tendency for sexual aggregation was scored on the three-point scale proposed by Estes (1991a) and Roberts (1996): (1) never in mixed-sex herds; (2) occasionally forming mixed-sex herds; and (3) regularly forming mixed-sex herds. A score of 1 was assigned to all those species which never aggregate into social groups containing multiple males and females. These included species with males either solitary or living in segregated, unisexual social groups, and only joining female herds in search of mating opportunities. All bovids with males associating seasonally with female herds, often during migrations and other mass movements, or after a breakdown of territorial systems following the end of the breeding season, received a score of 2. I assigned a value of 3 to the species in sexually-aggregated herds always containing multiple adult males (although some males can temporarily join bachelor groups; Jarman 1974, 1983). The scoring was based on available published material (Appendix).

Habitat openness was scored as the probability of detection of large mammals in each of the nine different IUCN habitat categories (www.iucnredlist.org), provided by Cabrera & Stankowich (2018): tropical forest (0.1), temperate forest (0.2), wetland (0.3), tropical shrubland (0.5), temperate shrubland (0.6), savannah (0.7), grassland (0.8); rocky areas (0.8), and desert (0.95). The overall score of habitat openness was considered as the average of detection probabilities across all habitat categories (Cabrera & Stankowich 2018).

Statistical analyses

All analyses were conducted in R 3.5.2 (R Development Core Team 2019), with the packages ape (Paradis et al. 2019) and caper (Orme et al. 2018) loaded in the main workspace. I applied the Phylogenetic Least Squares (pGLS) method to identify statistically significant predictors of colour and pelage dimorphism (Freckleton, Harvey & Pagel 2002; Mundry 2014). The pGLS approach takes into account data autocorrelation generated by shared ancestry, as it includes phylogeny (in the form of a variance-covariance matrix of branch lengths) in the error structure of an ordinary least squares regression model (Freckleton et al. 2002). The molecular-based phylogenetic tree adopted for this study was derived from Bininda-Edmonds et al. (2007), and pruned to include only the species included in the dataset. Branch lengths were scaled according to Pagel's lambda (Freckleton et al. 2002) set to a maximum likelihood estimate, and selected as the best fitting branch transformation to the dataset using the profile.pgls function in the package caper (Orme et al. 2018). Delta and kappa branch transformations produced qualitatively similar results (not reported here).

Colour and pelage dimorphism were modelled as response variables in separate pGLS models. Explanatory variables in all models included: (i) breeding group size; (ii) male mating strategy; (iii) sexual association; and (iv) habitat openness. Model simplification was implemented by removal of predictors in order of least significance (significance level set at $p \leq 0.05$; Murtaugh 2014). Coefficient estimates for non-significant predictors were obtained by adding each of them separately to the final model. Assumptions of residual normality and heteroscedasticity were graphically inspected using the plot.pgls function in the package caper (Orme et al. 2018). Normal residual distribution was achieved after log-transformation (with the formula $\log(x+1)$ when dimorphism scores equalled zero) of all continuous variables in the model for colour dimorphism, and square-root transformation for pelage dimorphism. Variance Inflation Factors (VIFs) were calculated in order to account for multicollinearity between explanatory variables (Kutner, Nachtsheim &

Neter 2005). All VIFs were ≤ 3, and thus well below the accepted threshold of concern (5-10; Kutner et al. 2005).

3.3 RESULTS

The degree of both colour and pelage dimorphism in male bovids was significantly predicted by breeding group size, male mating strategy, and sexual aggregation in multivariate analyses (colour dimorphism: $F_{3,83}$ = 20.320; λ= 0.066; p = <0.001; R^2 = 0.403; pelage dimorphism: $F_{3,83}$ = 4.785; λ = 0.952; p = 0.003; R^2 = 0.117; **Table 2**; **Table 3**). The two components of morphological dimorphism were positively correlated with breeding group size and non-territorial mating strategies, as predicted by the Sexual Selection Hypothesis (**Figure 2**). Only 4 of 64 territorial species exhibited some form of colour dimorphism, in contrast to 26 of the 46 non-territorial species. Similarly, pelage dimorphism characterized 19 of 46 non-territorial bovids, but only one out of 64 territorial species (the sable antelope *Hippotragus niger*). Additionally, the magnitude of both traits was negatively correlated with the level of sexual aggregation (**Table 2**; **Table 3**), supporting the Social Integration hypothesis. None of the species that regularly aggregate in mixed-sex herds were scored as morphologically dimorphic (**Figure 3**). Habitat openness did not show any significant correlations with neither colour nor pelage dimorphism (**Table 2**; **Table 3**), contrary to expectations from the Habitat-Mediated Selection hypothesis.

3.4 DISCUSSION

This study provides comparative evidence that sexual dimorphism in two morphological traits of bovids, namely colouration and pelage ornaments, is promoted by sexual selection on males. In particular, the degree of morphological dimorphism was found to be positively correlated with the size of the breeding group and non-territorial mating strategies - two indicators of the level of male polygyny (a key determinant of the intensity of sexual selection). My findings also revealed negative correlations between morphological dimorphism and the tendency to form mixed-sex herds, suggesting a limiting effect of social integration on the evolution of male ornaments.

Male territoriality characterizes the majority of bovids (63%) and the reduced colour and pelage dimorphism found in these species may derive from a smaller potential for polygyny (Gosling 1986; Bro-Jørgensen 2007; Cassini 2020). A parallel can be drawn with male weapons (horns and antlers), which are generally shorter and less elaborate in territorial ungulates (Bro-Jørgensen 2007; Plard, Bonenfant & Gaillard 2011). Furthermore, the virtual absence of morphological dimorphism in several highly polygynous antelopes which defend territories (e.g. Alpine chamois *Rupicapra rupicapra*; impala *Aepyceros melampus*; Jarman 1979; Corlatti et al. 2015) corroborates my hypothesis that sexual selection in territorial systems could target male traits other than ornaments. Specifically, it is possible that territoriality has favoured the evolution of male displays more suited to advertise territory occupancy (e.g. scent marks; vocalizations; Owen-Smith 1977; Gosling 1982), over ornamentation.

Their almost exclusive association with non-territoriality, on the other hand, implies that male dimorphic ornaments have been selected through their signalling function in sexual competition. In non-territorial breeding systems, the outcome of male confrontations plays a larger role than female mate choice in determining mating success, as a consequence of enforced copulations by dominant individuals (e.g. Coltman et al. 2002; Pelletier, Hogg & Festa-Bianchet 2006; Mainguy et al. 2008; Ihl & Bowyer 2011). This suggests that male colour and pelage ornaments could prove advantageous as displays of social status and other aspects of competitive ability, establishing male dominance rank without the need for costly fighting (Walther 1984; Loehr et al. 2008; Caro 2009; Holekamp & Strauss 2016; Bowyer et al. 2020). Support for this interpretation comes from several field studies. For example, fluctuations in the hue and size of pelage structures in male eland (*Tragelaphus oryx*) and Himalayan tahr (*Hemitragus jemlahicus*) mirror gains and losses in dominance rank (Bro-Jørgensen & Dabelsteen 2008; Bro-Jørgensen & Beeston 2015; Lovari et al. 2009, 2015). Male colours and other ornaments advertising social status are also associated with dominance-base mating strategies in other mammals (e.g. primates: Setchell & Jean Wickings 2005; Bergman, Ho & Beehner 2009; Petersdorf et al. 2017): non-territoriality could therefore represent an important driver of morphological dimorphism across different taxonomic groups.

The study found morphological dimorphism in bovids to be weaker in species where males and females aggregated into mixed-sex groups, irrespectively of the intensity of sexual selection. This is exemplified by the absence of dimorphic ornaments across all bovids living permanently in mixed-sex herds (African buffalo *Syncerus caffer*, muskox *Ovibos moschatus*, and oryx *Oryx* spp. and addax *Addax nasomaculatus* antelopes), despite the expected high levels of male polygyny due to large breeding groups and male non-territoriality (Walther 1978; Prins 1996; Forchhammer & Boomsma 1998). Some of highest scores of dimorphism were conversely assigned to species that were probably less polygynous (due to smaller group size), but usually segregated in unisexual herds (e.g. sitatunga *Tragelaphus spekii*; greater kudu *Tragelaphus strepsiceros*; Owen-Smith 1984; Estes 1991b). Analogous variation can be observed within species: for example, sexually-segregated mountain bongo antelopes (*Tragelaphus eurycerus isaaci*), exhibit distinctive male colourations, while the aggregated lowland subspecies (*T. e. eurycerus*) is monomorphic (Hillman 1986; Estes 1991b). These patterns indicate that male ornaments impose substantial costs in mixed-sex herds, offsetting the fitness benefits in sexual signalling.

My findings support that social integration constitutes a powerful selection regime promoting sexual monomorphism in colour and pelage. However, which specific advantages would males in mixed-sex herds gain from the lack of dimorphic ornaments? In schooling fish, males and females living in the same groups converge on similar phenotypes, as “confusion effects” generated by multiple, indistinguishable targets decrease the attack success of predators (Penry-Williams, Ioannou & Taylor 2018; Rystrom et al. 2018). Since similar confusion-based antipredator tactics are also employed by gregarious bovids (Kruuk 1972; FitzGibbon 1990; Caro 2005b), I propose here that monomorphism in mixed-sex herds might conceivably buffer males against selective predation. Strengthening this interpretation, my data show that morphological dimorphism is very rare (n = 4) in species with males joining female herds at critical times of the year (e.g. during seasons of resource shortage or mass movements), when exposure to predation risk is maximized (Fryxell, Greever & Sinclair 1988; Owen-Smith 2008). Other observations suggest an anti-harassment function for sexual uniformity. Visual resemblance to females apparently ensures that subordinate males are tolerated in mixed-sex herds and not forcedly evicted by dominant individuals, as long as they forego mating attempts (e.g. in the African buffalo and in the southern oryx; Sinclair 1977; Walther 1978). Nevertheless, sexual identity is often detected through olfactory cues, and this may possibly compromise the screening effect of female-like morphologies against aggression (Gosling & Roberts 2001). Additional research is therefore necessary to clarify selective benefits of sexual monomorphism.

A potential shortcoming of the social integration hypothesis arises from considering that morphological dimorphism in bovids also includes differences in horn length and shape, not included in the present study. Despite these concerns, horns appear to be less dimorphic in species forming mixed-sex herds (see Jarman 1983; Estes 1991b; Roberts 1996, although the function of female horns is debated), thereby conforming to the general trend for monomorphism as a consequence of sexual aggregation.

It is possible that social integration constitutes a more pervasive evolutionary force than previously thought, as it could explain the absence of dimorphic ornaments across several other taxa. In mammals, it is tempting to link the surprising absence of morphological dimorphism in highly polygynous lineages, such as equids, kangaroos, and some primates (e.g. savannah baboons *Papio* spp. Jarman 1983; Dixson, Dixson & Anderson

2005), with their tendency to aggregate in mixed-sex groups. Future comparative studies on sexual dimorphism should thus take into account social integration as a potential limiting factor on sexual selection.

No evidence was found for a positive correlation between morphological dimorphism and habitat openness. Surprisingly, some antelopes associated with relatively dense habitat types (habitat openness <0.5), and generally employing cryptic behaviour to avoid predators, exhibited some of the most dimorphic ornamentation among bovids (e.g. *Tragelaphus* antelopes; Estes 1991b). It is likely that the observed association between sexual monomorphism and dense habitats (e.g. Estes 2000) spuriously emerged as a consequence of smaller breeding group size, and incidentally restricted opportunities for sexual selection, in forest species (Jarman 1974).

3.5 CONCLUSION

I found that interspecific variation in morphological dimorphism among bovids reflects underlying differences in the intensity of sexual selection, and in the degree of sexual aggregation. In particular, whereas male mating competition promotes the evolution of dimorphic ornaments, social integration in mixed-sex herds seemingly exerts a contrasting selection pressure towards sexual monomorphism. It is now necessary to test the wider applicability of social integration as an explanation for attenuated morphological dimorphism in other taxonomic groups.

3.6 TABLES

Table 1: Hypotheses and predictions for the evolution of morphological dimorphism in bovids. Symbols in cells refers to the expected correlation between the degree of colour and pelage dimorphism, and selected independent variables (0 = no correlation; + = positive correlation; - = negative correlation).

	Predictors of morphological dimorphism			
Hypotheses	Group size	Mating strategy	Sexual Aggregation	Habitat Openness
Sexual selection	+	+ (non-territorial)	0	0
Social integration	0	0	-	0
Habitat-mediated Selection	0	0	0	+

Table 2: PGLS correlations between the degree of colour dimorphism in bovids and various socio-ecological traits. Coefficients estimates and statistical significance are provided for a multivariate model containing all significant predictors ($F_{3,83} = 20.320$; $\lambda = 0.066$; $p = <0.001$; $R^2 = 0.403$).

	Coefficient	S.E.	t	P
Group Size (log)	0.261	0.081	3.213	**0.002**
Non-territorial Mating Strategy	0.795	0.172	4.621	**<0.001**
Sexual Aggregation	-0.772	0.161	-4.791	**<0.001**
Habitat Openness	-0.386	0.382	-1.012	0.314

Table 3: PGLS correlations between degree of dimorphism in pelage ornaments in bovids and various socio-ecological traits. Coefficients estimates and statistical significance are provided for a multivariate model containing all significant predictors ($F_{3,83} = 4.785$; $\lambda = 0.952$; $p = 0.003$; $R^2 = 0.117$).

	Coefficient	S.E.	t	P
Group Size (log)	0.076	0.037	2.064	**0.042**
Non-Territorial Mating Strategy	0.517	0.232	2.232	**0.028**
Sexual Aggregation	-0.326	0.117	-2.793	**0.006**
Habitat Openness	-0.263	0.318	-0.828	0.501

3.7 FIGURES

Figure 1: Bovid hair colour based on the dominant type of pigment (i.e. no pigment, phaeomelanin, or eumelanin). For each colour category, different gradations are presented as examples of variability in pigment saturation. Bovids were conservatively scored as dimorphic for differences between these categories. This classification was based on examination of high-quality pictures where single hair could be easily detected by the naked eye.

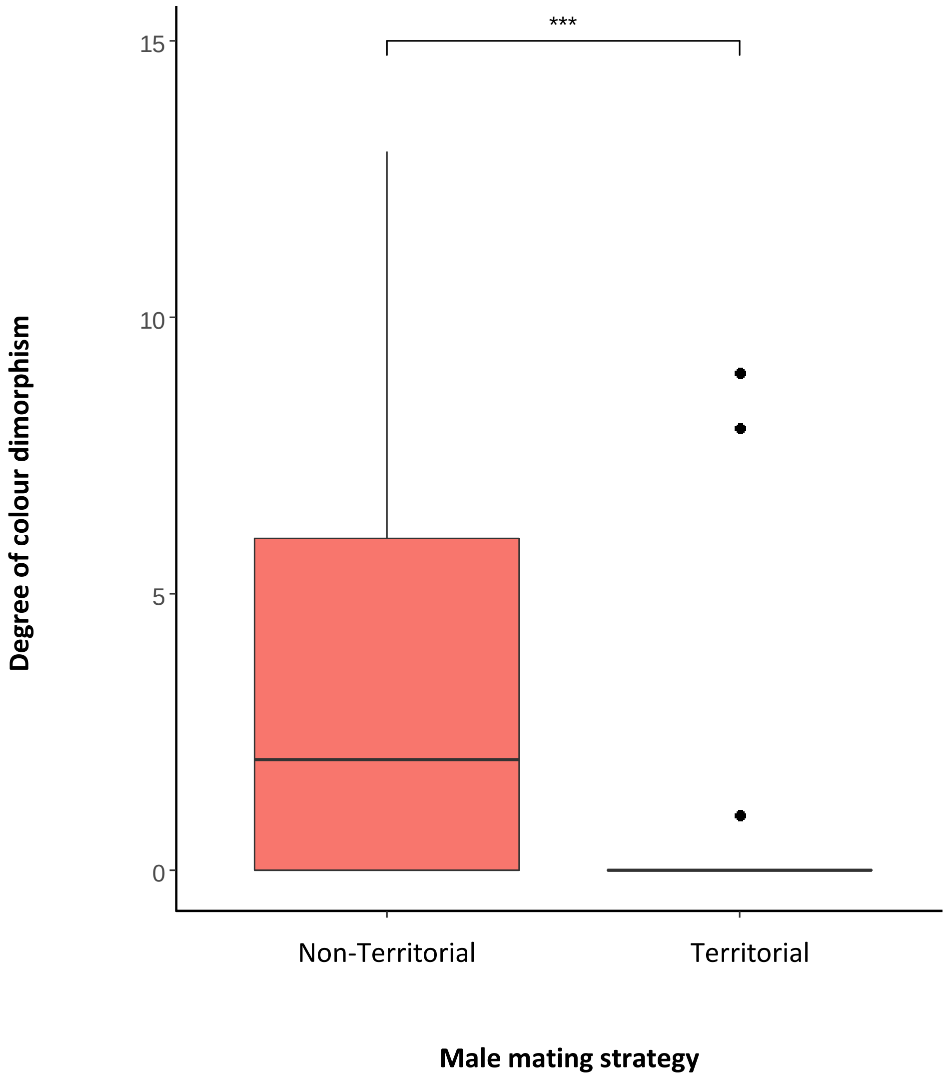
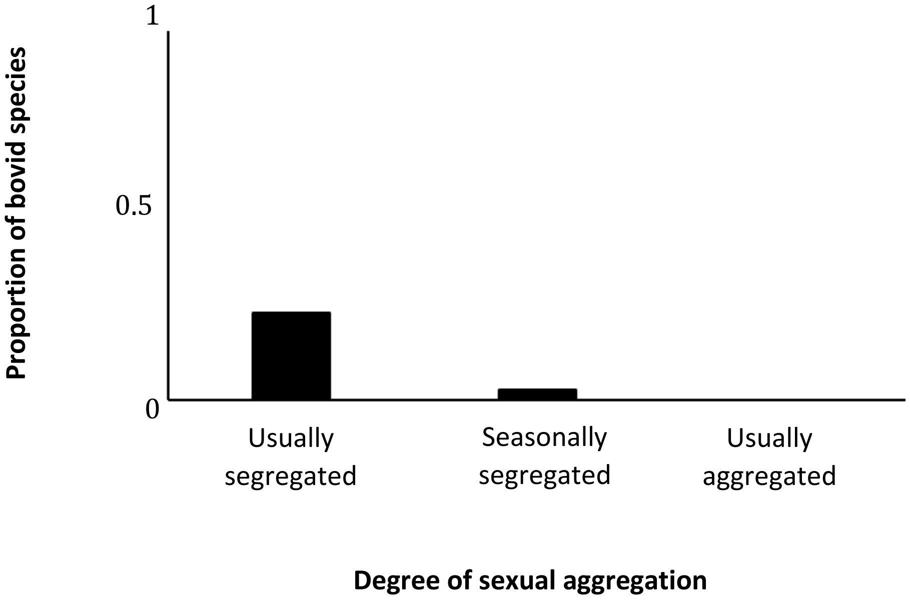
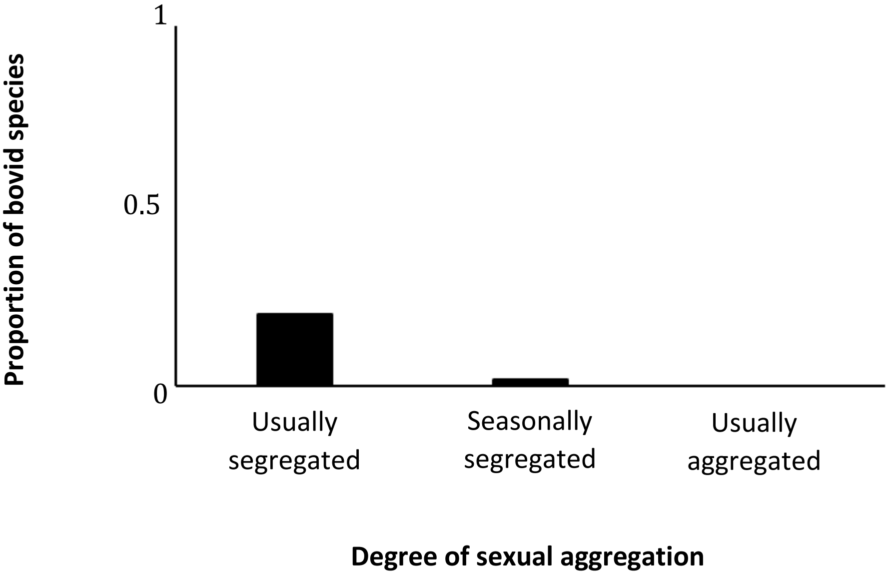


Figure 2: Colouration dimorphism in bovid species with territorial (T) and non-territorial (NT) male mating strategies.



(A) Colour dimorphism



(B) Pelage ornaments dimorphism

Figure 3: Proportion of colour (A) and pelage (B) dimorphic species according to sexual aggregation (n = 110).

3.8 REFERENCES

Andersson, M. (1994). *Sexual selection*. Princeton University Press.

Andersson, M., & Iwasa, Y. (1996). Sexual selection. *Trends in Ecology & Evolution*, **11**(2), 53-58.

Andersson, M., & Simmons, L. W. (2006). Sexual selection and mate choice. *Trends in Ecology & Evolution*, **21**(6), 296-302.

Badyaev, A. V., & Hill, G. E. (2000). Evolution of sexual dichromatism: contribution of carotenoid-versus melanin-based coloration. *Biological Journal of the Linnean Society*, **69**(2), 153-172.

Balmford, A., Rosser, A. M., & Albon, S. D. (1992). Correlates of female choice in resource-defending antelope. *Behavioral Ecology and Sociobiology*, **31**(2), 107-114.

Bergman, T. J., Ho, L., & Beehner, J. C. (2009). Chest color and social status in male geladas (*Theropithecus gelada*). *International Journal of Primatology*, **30**(6), 791-806.

Bininda-Emonds, O. R., Cardillo, M., Jones, K. E., MacPhee, R. D., Beck, R. M., Grenyer, R., & Purvis, A. (2007). The delayed rise of present-day mammals. *Nature*, **446**(7135), 507-512.

Bossu, C. M., & Near, T. J. (2015). Ecological constraint and the evolution of sexual dichromatism in darters. *Evolution*, **69**(5), 1219-1231.

Bowyer, R. T., McCullough, D. R., Rachlow, J. L., Ciuti, S., & Whiting, J. C. (2020). Evolution of ungulate mating systems: Integrating social and environmental factors. *Ecology and Evolution*. In press.

Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication*. Sinauer.

Bro-Jørgensen, J. (2002). Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences*, **99**(14), 9290-9293.

Bro-Jørgensen, J. (2007). The intensity of sexual selection predicts weapon size in male bovids. *Evolution*, **61**(6), 1316-1326.

Bro-Jørgensen, J. (2011). Intra-and intersexual conflicts and cooperation in the evolution of mating strategies: lessons learnt from ungulates. *Evolutionary Biology*, **38**(1), 28-41.

Bro-Jørgensen, J., & Dabelsteen, T. (2008). Knee-clicks and visual traits indicate fighting ability in eland antelopes: multiple messages and back-up signals. *BMC Biology*, **6**(1), 47.

Bro-Jørgensen, J., & Beeston, J. (2015). Multimodal signalling in an antelope: fluctuating facemasks and knee-clicks reveal the social status of eland bulls. *Animal Behaviour*, **102**, 231-239.

Cabrera, D., & Stankowich, T. (2018). Stabbing Slinkers: Tusk Evolution Among Artiodactyls. *Journal of Mammalian Evolution*, 8.

Caro, T. (2005a). *Antipredator defenses in birds and mammals*. University of Chicago Press.

Caro, T. I. M. (2005b). The adaptive significance of coloration in mammals. *BioScience*, **55**(2), 125-136.

Caro, T. (2009). Contrasting coloration in terrestrial mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**(1516), 537-548.

Caro, T. M., Graham, C. M., Stoner, C. J., & Vargas, J. K. (2004). Adaptive significance of antipredator behaviour in artiodactyls. *Animal behaviour*, **67**(2), 205-228.

Caro, T., & Stankowich, T. (2010). The function of contrasting pelage markings in artiodactyls. *Behavioral Ecology*, **21**(1), 78-84.

Caro, T., Walker, H., Rossman, Z., Hendrix, M., & Stankowich, T. (2017). Why is the giant panda black and white?. *Behavioral Ecology*, **28**(3), 657-667.

Caro, T., Newell, C., & Stankowich, T. (2018). Ecocorrelates of pelage coloration in pigs and peccaries. *Journal of Mammalogy*, **99**(5), 1093-1100.

Cassini, M. H. (2020). Sexual size dimorphism and sexual selection in artiodactyls. *Behavioral Ecology*. In press.

Clutton-Brock, T. H., Albon, S. D., & Harvey, P. H. (1980). Antlers, body size and breeding group size in the Cervidae. *Nature*, **285**(5766), 565-567.

Clutton-Brock, T. H., Green, D., Hiraiwa-Hasegawa, M., & Albon, S. D. (1988). Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behavioral Ecology and Sociobiology*, **23**(5), 281-296.

Clutton-Brock, T. H., Deutsch, J. C., & Nefdt, R. J. C. (1993). The evolution of ungulate leks. *Animal Behaviour*, **46**(6), 1121-1138.

Coltman, D. W., Festa-Bianchet, M., Jorgenson, J. T., & Strobeck, C. (2002). Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **269**(1487), 165-172.

Cooney, C. R., Varley, Z. K., Nouri, L. O., Moody, C. J., Jardine, M. D., & Thomas, G. H. (2019). Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. *Nature Communications*, **10**(1), 1-9.

Costello, J. R. (2016). *Bovids of the world*. Princeton University Press.

Corlatti, L., Bassano, B., Poláková, R., Fattorini, L., Pagliarella, M. C., & Lovari, S. (2015). Preliminary analysis of reproductive success in a large mammal with alternative mating tactics, the Northern chamois, *Rupicapra rupicapra*. *Biological Journal of the Linnean Society*, **116**(1), 117-123.

Darwin, C. (1871). *The descent of man, and selection in relation to sex*. John Murray, London.

Dixson, A., Dixson, B., & Anderson, M. (2005). Sexual selection and the evolution of visually conspicuous sexually dimorphic traits in male monkeys, apes, and human beings. *Annual review of sex research*, **16**(1), 1-19.

Estes, R. D. (1991a). *The behaviour guide to African mammals: including hoofed mammals, carnivores, primates*. Russell Friedman Books CC, Johannesburg.

Estes, R. D. (1991b). The significance of horns and other male secondary sexual characters in female bovids. *Applied Animal Behaviour Science*, *29*(1), 403-451.

Estes, R. D. (2000). Evolution of conspicuous coloration in the Bovidae: female mimicry of male secondary sexual characters as a catalyst. In Schaller, G.B., & Vrba, E. S. (Eds). *Antelopes, deer and relatives*. Yale University Press, New Haven & London.

Fitzgibbon, C. D. (1990). Why do hunting cheetahs prefer male gazelles?. *Animal Behaviour*, **40**(5), 837-845.

Forchhammer, M. C., & Boomsma, J. J. (1998). Optimal mating strategies in nonterritorial ungulates: a general model tested on muskoxen. *Behavioral Ecology*, **9**(2), 136-143.

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**(6), 712-726.

Fryxell, J. M., Greever, J., & Sinclair, A. R. E. (1988). Why are migratory ungulates so abundant?. *The American Naturalist*, **131**(6), 781-798.

Geist, V. (1968). On delayed social and physical maturation in mountain sheep. *Canadian Journal of Zoology*, **46**(5), 899-904.

Geist, V. (1974). On the relationship of social evolution and ecology in ungulates. *American Zoologist*, **14**(1), 205-220.

Geist, V. (1977). A comparison of social adaptations in relation to ecology in gallinaceous bird and ungulate societies. *Annual Review of Ecology and Systematics*, **8**(1), 193-207.

Geist, V., & Bayer, M. (1988). Sexual dimorphism in the Cervidae and its relation to habitat. *Journal of Zoology*, **214**(1), 45-53.

Geist, V., & Bromley, P.T. (1978). Why deer shed antlers. *Zeitschrift fur Saugertierkunde*, **43**(4), 223-231.

Gosling, L. M. (1982). A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie*, **60**(2), 89-118.

Gosling, L. M. (1986). The evolution of mating strategies in male antelopes. In D. I. Rubenstein and R. W. Wrangham (eds), 244-281. Princeton University Press, Princeton, New Jersey.

Gosling, L. M., & Roberts, S. C. (2001). Scent-marking by male mammals: cheat-proof signals to competitors and mates. In *Advances in the Study of Behavior* (Vol. 30, pp. 169-217). Academic Press.

Grueter, C. C., Isler, K., & Dixson, B. J. (2015). Are badges of status adaptive in large complex primate groups?. *Evolution and Human Behavior*, **36**(5), 398-406.

Hillman, J. C. (1986). Aspects of the biology of the bongo antelope *Tragelaphus eurycerus* Ogilby 1837 in south west Sudan. *Biological Conservation*, **38**(3), 255-272.

Holekamp, K. E., & Strauss, E. D. (2016). Aggression and dominance: an interdisciplinary overview. *Current Opinion in Behavioral Sciences*, **12**, 44-51.

Ihl, C., & Bowyer, R. T. (2011). Leadership in mixed-sex groups of muskoxen during the snow-free season. *Journal of Mammalogy*, **92**(4), 819-827.

Isvaran, K. (2005). Variation in male mating behaviour within ungulate populations: patterns and processes. *Current Science*, 1192-1199.

Jarman, P. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, **48**(1-4), 215-267.

Jarman, M. V. (1979). *Impala social behaviour: territory, hierarchy, mating, and the use of space*. Parey.

Jarman, P. (1983). Mating system and sexual dimorphism in large terrestrial, mammalian herbivores. *Biological Reviews*, **58**(4), 485-520.

Kruuk, H. (1972). *The spotted hyena: a study of predation and social behaviour*. The University of Chicago Press, Chicago, USA.

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

Kutner, M. H., Nachtsheim, C. J., Neter, J., & Li, W. (2005). *Applied linear statistical models* (Vol. 5). McGraw-Hill Irwin, New York.

Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**(2), 292-305.

Lande, R., & Arnold, S. J. (1985). Evolution of mating preference and sexual dimorphism. *Journal of Theoretical Biology*, **117**(4), 651-664.

Landeau, L., & Terborgh, J. (1986). Oddity and the 'confusion effect'in predation. *Animal Behaviour*, **34**(5), 1372-1380.

Loehr, J., Carey, J., Ylönen, H., & Suhonen, J. (2008). Coat darkness is associated with social dominance and mating behaviour in a mountain sheep hybrid lineage. *Animal Behaviour*, *76*(5), 1545-1553.

Lovari, S., Pellizzi, B., Boesi, R., & Fusani, L. (2009). Mating dominance amongst male Himalayan tahr: blonds do better. *Behavioural Processes*, **81**(1), 20-25.

Lovari, S., Fattorini, N., Boesi, R., & Bocci, A. (2015). Male ruff colour as a rank signal in a monomorphic-horned mammal: behavioural correlates. *The Science of Nature*, **102**(7-8), 39.

Lüpold, S., Simmons, L. W., & Grueter, C. C. (2019). Sexual ornaments but not weapons trade off against testes size in primates. *Proceedings of the Royal Society B*, **286**(1900), 20182542.

Main, M. B., & Coblentz, B. E. (1990). Sexual segregation among ungulates: a critique. *Wildlife Society Bulletin*, **18**(2), 204-210.

Mainguy, J., Côté, S. D., Cardinal, E., & Houle, M. (2008). Mating tactics and mate choice in relation to age and social rank in male mountain goats. *Journal of Mammalogy*, **89**(3), 626-635.

McCullough, E. L., Miller, C. W., & Emlen, D. J. (2016). Why sexually selected weapons are not ornaments. *Trends in Ecology & Evolution*, **31**(10), 742-751.

Møller, A. P., & Pomiankowski, A. (1993). Why have birds got multiple sexual ornaments?. *Behavioral Ecology and Sociobiology*, **32**(3), 167-176.

Mundry, R. (2014). Statistical issues and assumptions of phylogenetic generalized least squares. In *Modern Phylogenetic Comparative Methods and their Application in Evolutionary Biology*, 131-153. Springer, Berlin, Heidelberg.

Murtaugh, P. A. (2014). In defense of P values. *Ecology*, **95**(3), 611-617.

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., & Fritz, S. (2018). The caper package: comparative analysis of phylogenetics and evolution in R. *R package version*, **5**(2), 1-36.

Owen-Smith, N. (1977). On territoriality in ungulates and an evolutionary model. *The Quarterly Review of Biology*, **52**(1), 1-38.

Owen-Smith, N. (1984). Spatial and temporal components of the mating systems of kudu bulls and red deer stags. *Animal Behaviour*, **32**(2), 321-332.

Owen-Smith, N. (2008). Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos*, **117**(4), 602-610.

Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claude, J., Cuong, H. S., & Desper, R. (2019). Package 'ape'. *Analyses of Phylogenetics and Evolution,* **2**(4).

Pelletier, F., Hogg, J. T., & Festa-Bianchet, M. (2006). Male mating effort in a polygynous ungulate. *Behavioral Ecology and Sociobiology*, **60**(5), 645-654.

Penry-Williams, I. L., Ioannou, C. C., & Taylor, M. I. (2018). The oddity effect drives prey choice but not necessarily attack time. *Ethology*, **124**(7), 496-503.

Pérez-Barbería, F. J., Gordon, I. J., & Pagel, M. (2002). The origins of sexual dimorphism in body size in ungulates. *Evolution*, **56**(6), 1276-1285.

Petersdorf, M., Dubuc, C., Georgiev, A. V., Winters, S., & Higham, J. P. (2017). Is male rhesus macaque facial coloration under intrasexual selection?. *Behavioral Ecology*, **28**(6), 1472-1481.

Plard, F., Bonenfant, C., & Gaillard, J. M. (2011). Revisiting the allometry of antlers among deer species: male–male sexual competition as a driver. *Oikos*, **120**(4), 601-606.

Price, T. D. (2017). Sensory drive, color, and color vision. *The American Naturalist*, **190**(2), 157-170.

Prins, H. (1996). *Ecology and behaviour of the African buffalo: social inequality and decision making*. Springer Science & Business Media.

R Development Core Team (2019). A language environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Roberts, S. C. (1996). The evolution of hornedness in female ruminants. *Behaviour*, **133**(5-6), 399-442.

Rystrom, T. L., Clement, V. F., Rick, I. P., Bakker, T. C., & Mehlis, M. (2018). Shoal sex composition and predation risk influence sub-adult threespine stickleback shoaling decisions. *Behavioural Processes*, **157**, 495-501.

Schaller, G. B. (1977). *Mountain Monarchs. Wild sheep and Goats of the Himalaya*. University of Chicago Press.

Setchell, J. M., & Jean Wickings, E. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology*, **111**(1), 25-50.

Shultz, A. J., & Burns, K. J. (2017). The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (Aves: Thraupidae). *Evolution*, **71**(4), 1061-1074.

Shuster, S. M. (2009). Sexual selection and mating systems. *Proceedings of the National Academy of Sciences*, **106**(1), 10009-10016.

Sinclair, A. R. E. (1977). The African buffalo; a study of resource limitation of populations.

Stoner, C. J., Caro, T. M., & Graham, C. M. (2003). Ecological and behavioral correlates of coloration in artiodactyls: systematic analyses of conventional hypotheses. *Behavioral Ecology*, **14**(6), 823-840.

Stuart–Fox, D. M., & Ord, T. J. (2004). Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**(1554), 2249-2255.

Vanpé, C., Kjellander, P., Galan, M., Cosson, J. F., Aulagnier, S., Liberg, O., & Hewison, A. M. (2008). Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. *Behavioral Ecology*, **19**(2), 309-316.

Vanpé, C., Morellet, N., Kjellander, P., Goulard, M., Liberg, O., & Hewison, A. M. (2009). Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality. *Journal of Animal Ecology*, **78**(1), 42-51.

Wade, M. J., & Shuster, S. M. (2004). Sexual selection: harem size and the variance in male reproductive success. *The American Naturalist*, **164**(4), E83-E89.

Walther, F. R. (1978). Behavioral observations on oryx antelope (*Oryx beisa*) invading Serengeti National Park, Tanzania. *Journal of Mammalogy*, **59**(2), 243-260.

Walther, F. R. (1984). *Communication and expression in hoofed mammals*. Indiana University Press.

Weckerly, F. W. (1998). Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy*, **79**(1), 33-52.

Zuk, M., & Kolluru, G. R. (1998). Exploitation of sexual signals by predators and parasitoids. *The Quarterly Review of Biology*, **73**(4), 415-438.

3.9 APPENDIX

Dataset

Species	Colour dimorphism	Pelage dimorphism	Group size	Male mating strategy	Sexual aggregation	Habitat openness
Addax nasomaculatus	0	0	20	NT	3	0.950
Aepyceros melampus	0	0	20	T	2	0.750
Alcelaphus buselaphus	0	0	10	T	2	0.600
Ammodorcas clarkei	0	0	3	T	1	0.500
Ammotragus lervia	0	2	3	NT	1	0.716
Antidorcas marsupialis	0	0	24	T	2	0.767
Antilope cervicapra	8	0	23	T	1	0.800
Bison bison	2	3	57	NT	2	0.585
Bison bonasus	0	0	20	NT	1	0.400
Bos frontalis	6	0	9.5	NT	1	0.100
Bos grunniens	0	0	80	NT	2	0.875
Bos javanicus	6	0	21	NT	1	0.333
Boselaphus tragocamelus	11	2	7	NT	1	0.467
Bubalus bubalis	0	0	21	NT	2	0.333
Bubalus depressicornis	0	0	1	NT	1	0.100
Bubalus mindorensis	2	0	2	NT	1	0.460
Budorcas taxicolor	0	0	22.5	NT	2	0.500
Capra caucasica	0	3	12	NT	1	0.600
Capra cylindricornis	0	3	12	NT	1	0.600
Capra falconeri	6	8	9	NT	1	0.440
Capra hircus	13	6	15	NT	1	0.636
Capra ibex	0	3	15	NT	1	0.800
Capra nubiana	4	3	20	NT	1	0.825
Capra pyrenaica	8	3	10	NT	1	0.500
Capra sibirica	6	3	13.8	NT	1	0.788
Capra walie	5	3	20	NT	1	0.750
Cephalophus adersi	0	0	1.5	T	1	0.100
Cephalophus callipygus	0	0	1	T	1	0.100
Cephalophus dorsalis	0	0	1	T	1	0.100
Cephalophus jentinki	0	0	1	T	1	0.100
Cephalophus leucogaster	0	0	1	T	1	0.100
Cephalophus maxwellii	0	0	1.5	T	1	0.300
Cephalophus monticola	0	0	2	T	1	0.100
Cephalophus natalensis	0	0	2	T	1	0.230
Cephalophus niger	0	0	1	T	1	0.100
Cephalophus nigrifrons	0	0	1	T	1	0.200
Cephalophus rufilatus	0	0	1	T	1	0.400
Cephalophus silvicultor	0	0	2	T	1	0.230
Cephalophus zebra	0	0	1	T	1	0.100
Connochaetes gnou	0	0	21	T	2	0.700
Connochaetes taurinus	0	0	15	T	2	0.767
Damaliscus hunteri	0	0	18	T	2	0.800

Damaliscus lunatus	0	0	6	T	2	0.660
Damaliscus pygargus	0	0	8	T	2	0.667
Dorcatragus megalotis	0	0	5	T	1	0.650
Gazella cuvieri	0	0	4.5	T	1	0.600
Gazella dama	0	0	6	T	2	0.717
Gazella dorcas	0	0	17	T	2	0.750
Gazella gazella	0	0	6	T	1	0.875
Gazella granti	1	0	10	T	2	0.720
Gazella leptoceros	0	0	6	T	2	0.950
Gazella rufifrons	0	0	5	T	2	0.667
Gazella soemmerringii	0	0	7	T	2	0.667
Gazella spekei	0	0	8	T	1	0.750
Gazella subgutturosa	0	0	4	T	2	0.800
Gazella thomsonii	0	0	28	T	2	0.750
Hemitragus hylocrius	3	0	7	NT	1	0.800
Hemitragus jemlahicus	7	9	15	NT	1	0.440
Hippotragus equinus	0	0	13	T	1	0.525
Hippotragus niger	8	1	20	T	1	0.400
Kobus ellipsiprymnus	0	0	8	T	1	0.525
Kobus kob	0	0	25	T	1	0.575
Kobus leche	0	0	12	T	2	0.550
Kobus megaceros	9	2	25	T	1	0.575
Kobus vardonii	0	0	15	T	1	0.600
Litocranius walleri	0	0	3	T	1	0.700
Madoqua guentheri	0	0	2	T	1	0.500
Madoqua kirkii	0	0	2	T	1	0.500
Madoqua saltiana	0	0	2	T	1	0.300
Naemorhedus crispus	0	0	1	T	1	0.533
Naemorhedus goral	0	0	8	T	1	0.488
Naemorhedus_sumatraensis	0	0	1	T	1	0.375
Neotragus batesi	0	0	1.5	T	1	0.100
Neotragus moschatus	0	0	1.5	T	1	0.260
Neotragus pygmaeus	0	0	1.5	T	1	0.100
Oreamnos americanus	0	0	4	NT	1	0.600
Oreotragus oreotragus	0	0	2	T	1	0.625
Oryx dammah	0	0	12	NT	3	0.717
Oryx gazella	0	0	18.5	NT	3	0.738
Oryx leucoryx	0	0	15	NT	3	0.950
Ourebia ourebi	0	0	3	T	1	0.767
Ovibos moschatus	0	0	15	NT	3	0.800
Ovis ammon	1	3	50	NT	1	0.670
Ovis canadensis	0	0	10	NT	1	0.800
Ovis dalli	0	0	3.7	NT	1	0.783
Ovis vignei	2	3	63	NT	1	0.614
Pantholops hodgsonii	10	0	17	NT	1	0.800
Pelea capreolus	0	0	4	T	1	0.750
Procapra gutturosa	0	0	20	T	2	0.800
Pseudois nayaur	2	0	11.5	NT	1	0.783
Raphicerus campestris	0	0	1.5	T	1	0.620

Raphicerus melanotis	0	0	1	T	1	0.600
Raphicerus sharpei	0	0	1	T	1	0.600
Redunca arundinum	0	0	3	T	1	0.575
Redunca fulvorufula	0	0	4	T	1	0.800
Redunca redunca	0	0	4	T	1	0.800
Rupicapra rupicapra	0	0	20	T	2	0.600
Saiga tatarica	1	0	35	NT	2	0.875
Sylvicapra grimmia	0	0	2	T	1	0.594
Syncerus caffer	0	0	50	NT	3	0.488
Taurotragus derbianus	0	0	20	NT	2	0.400
Taurotragus oryx	6	3	45	NT	2	0.567
Tetracerus quadricornis	0	0	1	NT	1	0.230
Tragelaphus angasii	7	8	4	NT	1	0.430
Tragelaphus buxtoni	6	2	8	NT	1	0.467
Tragelaphus eurycerus	5	0	6	NT	1	0.300
Tragelaphus imberbis	7	3	5	NT	1	0.430
Tragelaphus scriptus	3	1	2	NT	1	0.300
Tragelaphus spekii	8	1	2	NT	1	0.314
Tragelaphus strepsiceros	6	4	16	NT	1	0.430

References

Ahrestani, F. S. (2018). Bos frontalis and Bos gaurus (Artiodactyla: Bovidae). *Mammalian Species*, **959**, 34-50.

Anderson, J. L. (1980). The social organisation and aspects of behaviour of the nyala *Tragelaphus angasi* Gray, 1849. *Zeitschrift für Säugetierkunde*, **19** (45), 141-152.

Annighöfer, P., & Schütz, S. (2011). Observations on the population structure and behaviour of two differently managed populations of the greater kudu (*Tragelaphus strepsiceros*, Pallas 1766) in Namibia. *European Journal of Wildlife Research*, **57**(4), 895-907.

Arcese, P., Jongejan, G., & Sinclair, A. R. E. (1995). Behavioural flexibility in a small African antelope: group size and composition in the oribi (*Ourebia ourebi*, Bovidae). *Ethology*, **99**(1-2), 1-23.

Baskaran, N., Kannan, V., Thiyagesan, K., & Desai, A. A. (2011). Behavioural ecology of four-horned antelope (*Tetracerus quadricornis* de Blainville, 1816) in the tropical forests of southern India. *Mammalian Biology*, **76**(6), 741-747.

Berger, J., & Cunningham, C. (1994). *Bison: mating and conservation in small populations*. Columbia University Press.

Bigalke, R. C. (1972). Observations on the behaviour and feeding habits of the springbok, *Antidorcas marsupialis*. *African Zoology*, **7**(1), 333-359.

Blank, D. A., Ruckstuhl, K. E., & Yang, W. (2012a). Sexual segregation in goitered gazelles (*Gazella subgutturosa*). *Canadian Journal of Zoology*, **90**(8), 955-960.

Blank, D., Ruckstuhl, K. E., & Yang, W. (2012b). Social organization in goitered gazelle (*Gazella subgutturosa* Güldenstaedt 1780). *Ethology Ecology & Evolution*, **24**(4), 306-321.

Bowyer, R. T., & Leslie, D. M. (1992). Ovis dalli. *Mammalian Species*, **393**, 1-7.

Bro-Jørgensen, J. (2007). The intensity of sexual selection predicts weapon size in male bovids. *Evolution*, **61**(6), 1316-1326.

Bro-Jørgensen, J. (2008). Dense habitats selecting for small body size: a comparative study on bovids. *Oikos*, **117**(5), 729-737.

Bro-Jørgensen, J. (2014). Will their armaments be their downfall? Large horn size increases extinction risk in bovids. *Animal Conservation*, **17**(1), 80-87.

Cain, J. W., Krausman, P. R., & Germaine, H. L. (2004). Antidorcas marsupialis. *Mammalian Species*, **753**, 1-7.

Cunningham, P., Plath, M., Wronski, T., & Sandouka, M. (2010). Differences in sexual dimorphism among four gazelle taxa (*Gazella* spp.) in the Middle East. *Animal Biology*, **60**(4), 395-412.

Custodio, C. C., Lepiten, M. V., & Heaney, L. R. (1996). Bubalus mindorensis. *Mammalian Species*, **520**, 1-5.

David, J. H. M. (1973). The behaviour of the bontebok, *Damaliscus dorcas dorcas*, (Pallas 1766), with special reference to territorial behaviour. *Zeitschrift für Tierpsychologie*, **33**(1), 38-107.Press.

David, J. H. M. (1978). Observations on territorial behaviour of springbok, *Antidorcas marsupialis*, in the Bontebok National Park, Swellendam. *African Zoology*, **13**(1), 123-141.

Dubost, G. (1980). L 'écologie et la vie sociale du Céphalophe bleu (*Cephalophus monticola* Thunberg), petit ruminant forestier africain. *Zeitschrift für Tierpsychologie*, **54**(3), 205-266.

Dubost, G., & Feer, F. (1988). Variabilité comportementale à l'intérieur du genre *Cephalophus* (Ruminantia, Bovidae), par l'exemple de *C. rufilatus* Gray, 1846. *Zeitschrift für Säugetierkunde*, **53**(1), 31-47.

Du Toit, J. T. (1995). Sexual segregation in kudu: sex differences in competitive ability, predation risk or nutritional needs? *South African Journal of Wildlife Research*, **25**(4), 127-132.

Estes, R. D. (1967). The comparative behavior of Grants and Thomson's gazelles. *Journal of Mammalogy*, **48**(2), 189-209.

Estes, R. D. (1969). Territorial behavior of the wildebeest (*Connochaetes taurinus* Burchell, 1823). *Zeitschrift für Tierpsychologie*, **26**(3), 284-370.

Estes, R. D. (1974). Social organization of the African Bovidae. In Geist, V., and Walther, F. R. (eds). *The behaviour of ungulates and its relation to management*, *1*, 166-205. IUCN, Morges, Switzerland.

Estes, R. D. (1991). *The behaviour guide to African mammals: including hoofed mammals, carnivores, primates*. Russell Friedman Books CC, Johannesburg.

Estes, R. D. (1991). The significance of horns and other male secondary sexual characters in female bovids. *Applied Animal Behaviour Science*, **29**(4), 403-451.

Estes, R. D., & Estes, R. K. (1974). The biology and conservation of the giant sable antelope, *Hippotragus niger variani* Thomas, 1916. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **126**. 73-104.

Fedosenko, A. K., & Blank, D. A. (2001). Capra sibirica. *Mammalian Species*, **675**, 1-13.

Fedosenko, A. K., & Blank, D. A. (2005). Ovis ammon. *Mammalian Species*, **773**, 1-15.

Feer, F., & Dubost, G. (1981). The behavior of the male *Antilope cervicapra* L., its development according to age and social rank. *Behaviour*, **76**(1-2), 62-125.

Frädrich, H. (1964). Beobachtungen zur Kreuzung zwischen Schwarzrückenducker*, Cephalophus dorsalis* Gray, 1846, und Zebraducker, *Cephalophus zebra* Gray, 1838. *Zeitschrift für Säugetierkunde*, **29**, 46-51.

Geist, V. (1965). On the rutting behavior of the mountain goat. *Journal of Mammalogy*, **45**(4), 551-568.

Geist, V. (1971). *Mountain sheep. A study in behavior and evolution*. University of Chicago Press.

Gosling, L. M. (1974). The social behaviour of Coke's hartebeest. In Geist, V., & Walther, F. R. (eds). *The behaviour of ungulates and its relation to management,* 1, 488-511. IUCN, Morges, Switzerland.

Grau, G. A., & Walther, F. R. (1976). Mountain gazelle agonistic behaviour. *Animal Behaviour*, **24**(3), 626-636.

Gray, D. R. (1987). *The muskoxen of Polar Bear Pass*. Fitzhenry & Whiteside, Markham, Ontario.

Gray, G. G., & Simpson, C. D. (1980). Ammotragus lervia. *Mammalian Species*, **144**, 1-7.

Grignolio, S., Rossi, I., Bassano, B., & Apollonio, M. (2007). Predation risk as a factor affecting sexual segregation in Alpine ibex. *Journal of Mammalogy*, **88**(6), 1488-1497.

Grobler, J.H. (1974). Aspects of the biology, population ecology and behaviour of the sable antelope *Hippotragus niger niger*, (Harris, 1838) in the Rhode Matopos National Park, Rhodesia. *Arnoldia,* **7**, 1–36.

Habibi, K. (1994). *The desert ibex: life history, ecology and behaviour of the Nubian ibex in Saudi Arabia*. National Commission for Wildlife Conservation and Development (NCWCD).

Habibi, K. (1997). Social behavior of the sand and mountain gazelle. In Habibi, K., Abuzinada, A. H., & Nader, A. I. (eds). *The gazelles of Arabia.* National Commission for Wildlife Conservation and Development (NCWCD).

Habibi, K., Thouless, C. R., & Lindsay, N. (1993). Comparative behaviour of sand and mountain gazelles. *Journal of Zoology*, **229**(1), 41-53.

Hillman, J. C. (1986). Aspects of the biology of the bongo antelope *Tragelaphus eurycerus* Ogilby 1837 in south west Sudan. *Biological Conservation*, **38**(3), 255-272.

Jarman, M. V. (1979). *Impala social behaviour: territory, hierarchy, mating, and the use of space*. Parey.

Jass, C. N., & Mead, J. I. (2004). Capricornis crispus. *Mammalian Species*, **750**, 1-10.

Jewell, P. A. (1972). Social organisation and movements of topi (*Damaliscus korrigum*) during the rut, at Ishasha, Queen Elizabeth Park, Uganda. *African Zoology*, **7**(1), 233-255.

Johnsingh, A. J. T., & Manjrekar, N. (Eds.). (2015). *Mammals of South Asia*. Universities Press India.

Joubert, S. C. J. (1974). The social organization of the roan antelope *Hippotragus equinus* and its influence on the spatial distribution of herds in the Kruger National Park. In Geist, V., and Walther, F. R. (eds). *The behaviour of ungulates and its relation to management*, *2*, 661-675. IUCN, Morges, Switzerland.

Jungius, H. (1971). The biology and behaviour of the reedbuck (*Redunca arundinum* Boddaert 1785) in the Kruger National Park. Parey, Hamburg und Berlin.

Kingdon, J. (1982). *East African mammals (bovids). Vol. 3, part C*. London Academic Press.

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., & Kalina, J. (eds). *Mammals of Africa* (Vol. 6), 340-346. A&C Black.

Kingswood, S. C., & Blank, D. A. (1996). Gazella subgutturosa. *Mammalian Species*, **518**, 1-10.

Kingswood, S. C., & Kumamoto, A. T. (1996). Madoqua guentheri. *Mammalian Species*, **539**, 1-10.

Kingswood, S. C., & Kumamoto, A. T. (1997). Madoqua kirkii. *Mammalian Species*, **569**, 1-10.

Krämer, A. (1969). Soziale organisation und sozialverhalten einer gemspopulation (*Rupicapra rupicapra* L.) der Alpen. *Zeitschrift für Tierpsychologie*, **26**(8), 889-964.

Kranz, K. R. (1991). Monogamy in the dik-dik. *Applied Animal Behaviour Science*, **29**(1-4), 87-105.

Krasińska, M., & Krasiński, Z. (1995). Composition, group size, and spatial distribution of European bison bulls in Białowieża Forest. *Acta Theriologica*, **40**(1), 1-21.

Krausman, P. R., & Casey, A. L. (2007). Addax nasomaculatus. *Mammalian Species*, **807**, 1-4.

Lent, P. C. (1969). A preliminary study of the Okavango lechwe*: Kobus leche leche* Gray. *African Journal of Ecology*, **7**(1), 147-157.

Lent, P. C. (1988). Ovibos moschatus. *Mammalian Species*, **302**, 1-9.

Leslie, D. M. (2008). Boselaphus tragocamelus. *Mammalian Species*, **813**, 1-16.

Leslie, D. M., & Schaller, G. B. (2008). Pantholops hodgsonii. *Mammalian Species*, **817**, 1-13.

Leslie, D. M., & Schaller, G. B. (2009). Bos grunniens and Bos mutus. *Mammalian species*, **836**, 1-17.

Leslie, D. M., & Sharma, K. (2009). Tetracerus quadricornis. *Mammalian Species*, **843**, 1-11.

Leuthold, W. (1978). On social organization and behaviour of the gerenuk *Litocranius walleri* (Brooke 1878). *Zeitschrift für Tierpsychologie*, **47**(2), 194-216.

Lobao-Tello, J. P., & Van Gelder, R. G. (1975). The natural history of nyala, *Tragelaphus angasi* (Mammalia, Bovidae) in Mozambique. *Bullettin of the American Museum of Natural History,* **155**(4), 323-385.

Lott, D. F. (1991). American bison socioecology. *Applied Animal Behaviour Science*, **29**(1-4), 135-145.

Lott, D. F. (2002). *American bison: a natural history* (Vol. 6). University of California Press.

Lovari, S., & Apollonio, M. (1994). On the rutting behaviour of the Himalayan goral *Nemorhaedus goral* (Hardwicke, 1825). *Journal of Ethology*, **12**(1), 25-34.

Lumpkin, S., & Kranz, K. R. (1984). Cephalophus sylvicultor. *Mammalian Species* **127**, 1-7.

Mainguy, J., & Côté, S. D. (2008). Age-and state-dependent reproductive effort in male mountain goats, *Oreamnos americanus*. *Behavioral Ecology and Sociobiology*, **62**(6), 935-943.

Masui, M. (1987). Social behaviour of Japanese serow, *Capricornis crispus crispus*. In Soma, H. (ed). *The Biology and Management of Capricornis and Related Mountain Antelopes*, 134-144. Springer, Dordrecht.

Mead, J. I. (1989). Nemorhaedus goral. *Mammalian Species*, **335**, 1-5.

Meagher, M. (1986). Bison bison. *Mammalian Species*, **266**, 1-8.

Mendelssohn, H., Yom-Tov, Y., & Groves, C. P. (1995). Gazella gazella. *Mammalian Species*, **490**, 1-7.

Mloszewski, M. J. (1983). *Behavior and ecology of the African buffalo*. Cambridge University Press.

Monfort-Braham, N. (1975). Variations dans la structure sociale du topi, *Damaliscus korrigum* Ogilby, au Pare National de l'Akagera, Rwanda. *Zeitschrift für Tierpsychologie*, **39**(5), 332-364.

Murray, M. G. (1981). Structure of association in impala, *Aepyceros melampus*. *Behavioral Ecology and Sociobiology*, **9**(1), 23-33.

Murray, M. G. (1982). Home range, dispersal and the clan system of impala. *African Journal of Ecology*, **20**(4), 253-269.

Neas, J. F., & Hoffmann, R. S. (1987). Budorcas taxicolor. *Mammalian Species*, **277**, 1-7.

Nievergelt, B. (1967). Die zusammensetzung der gruppen beim alpensteinbock. *Zeitschrift für Säugetierkunde*, **32**, 129-144.

Novellie, P. A., Manson, J., & Bigalke, R. E. (1984). Behavioural ecology and communication in the Cape grysbok. *African Zoology*, **19**(1), 22-30.

Pappas, L. A. (2002). Taurotragus oryx. *Mammalian Species*, **689**, 1-5.

Parrini, F., Cain, J. W., & Krausman, P. R. (2009). Capra ibex. *Mammalian Species*, **830**, 1-12.

Rai, D. (2019). Crowding, group size and population structure of the Blackbuck *Antilope cervicapra* (Linnaeus, 1758) (Mammalia: Cetartiodactyla: Bovidae) in the semi-arid habitat of Haryana, India. *Journal of Threatened Taxa*, **11**(9), 14194-14203.

Ralls, K. (1973). Cephalophus maxwellii. *Mammalian Species*, **31**, 1-4.

Ralls, K. (1978). Tragelaphus eurycerus. *Mammalian Species*, **111**, 1-4.

Rideout, C. B., & Hoffmann, R. S. (1975). Oreamnos americanus. *Mammalian Species*, **63**, 1-6.

Roberts, S. C. (1996). The evolution of hornedness in female ruminants. *Behaviour*, **133**(5-6), 399-442.

Ruckstuhl, K. E. (1998). Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour*, **56**(1), 99-106.

Ruckstuhl, K. E., & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews*, **77**(1), 77-96.

Ruso, G. E. (2017). Beatragus hunteri. *Mammalian Species*, **955**, 119-127.

Schaad, E. W., Wiseman, D. S., Huber, R. R., Mooring, M. S., Reisig, D. D., Osborne, E. R., & Hall, B. M. (2005). Sexual segregation in bison: a test of multiple hypotheses. *Behaviour*, **142**(7), 897-927.

Schaller, G. B. (1967). *The deer and the tiger*. University of Chicago Press.

Schaller, G. B. (1970). Observations on Nilgiri tahr (*Hemitragus hylocrius* Ogilby, 1838). *Journal of the Bombay Natural History Society*, **67**(3), 365-389.

Schaller, G. B. (1973). Observations on Himalayan tahr (*Hemitragus jemlahicus*). *Journal of the Bombay Natural History Society,* **70**, 1-24.

Schaller, G. B. (1973). On the behaviour of blue sheep (*Pseudois nayaur*). *Journal of the Bombay Natural History Society*, **69**, 523-537.

Schaller, G. B. (1977). *Mountain monarchs. Wild sheep and goats of the Himalaya*. University of Chicago Press.

Schaller, G. B. (2000). *Wildlife of the Tibetan steppe*. University of Chicago Press.

Schaller, G. B., & Mirza, Z. B. (1971). On the behavior of Kashmir markhor (*Capra falconeri cashmiriensis*). *Mammalia*, **35**(4), 548-566.

Schaller, G. B., & Mirza, Z. B. (1974). On the behaviour of Punjab urial (*Ovis orientalis punjabiensis*). In Geist, V., and Walther, F. R. (eds). *The behaviour of ungulates and its relation to management*, *1*, 306-323. IUCN, Morges, Switzerland.

Schaller, G. B., Junrang, R., & Mingjiang, Q. (1991). Observations on the Tibetan antelope (*Pantholops hodgsoni*). *Applied Animal Behaviour Science*, **29**(1-4), 361-378.

Schenkel, R. (1966). On sociology and behaviour in impala (*Aepyceros melampus lichtensteini*). *African Journal of Ecology*, **4**(1), 99-114.

Shackleton, D. M. (1985). Ovis canadensis. *Mammalian Species*, **230**, 1-9.

Shi, J., Li, X., Lu, F., Zhuge, H., & Dong, S. (2019). Variation in group sizes of sympatric Wild yak, Tibetan wild ass and Tibetan antelope in Arjin Shan National Nature Reserve of Xinjiang Province, China. *Global Ecology and Conservation*, **20**, e00749.

Sinclair, A. R. E. (1977*). The African buffalo; a study of resource limitation of populations*. University of Chicago Press, Chicago, USA.

Skinner, J. D., & Louw, G. N. (1996). *The Springbok: Antidorcas marsupialis (Zimmermann, 1780)*. Transvaal Museum.

Sokolov, V. E. (1974). Saiga tatarica. *Mammalian Species*, **38**, 1-4.

Sokolov, V. E., & Lushchekina, A. A. (1997). Procapra gutturosa. *Mammalian Species*, **571**, 1-5.

Spinage, C. (1982). *A territorial antelope: the Uganda waterbuck*. Elsevier.

Tener, J. S. (1965). *Muskoxen in Canada: a biological and taxonomic review* (Vol. 2). Department of Northern Affairs and National Resources, Canadian Wildlife Service.

Vats, R., & Bhardwaj, C. S. (2009). A Study of Reproductive Behaviour of Indian Black Buck (*Antilope cervicapra*) Linn. with Reference to Courtship, Breeding, Fawning and Colouration. *Current World Environment*, **4**(1), 121-125.

Von Richter, W. (1971). Observations on the biology and ecology of the black wildebeest (*Connochaetes gnou*). *South African Journal of Wildlife Research*, **1**(1), 3-16.

Von Richter, W. (1972). Territorial behaviour of the black wildebeest *Connochaetes gnou*. *African Zoology*, **7**(1), 207-231.

von Richter, W. (1974). Connochaetes gnou. *Mammalian Species*, **50**, 1-6.

Wang, X., & Hoffmann, R. S. (1987). Pseudois nayaur and Pseudois schaeferi. *Mammalian Species*, **278**, 1-6.

Walther, F. R. (1964). Einige Verhaltensbeobachtungen an Thomsongazellen (*Gazella thomsoni* Günther, 1884) im Ngorongoro-Krater. *Zeitschrift für Tierpsychologie*, **21**(7), 871-890.

Walther, F. (1964). Verhaltensstudien an der Gattung *Tragelaphus* de Blainville, 1816 in Gefangenschaft, unter besonderer Berücksichtigung des Sozialverhaltens. *Zeitschrift für Tierpsychologie*, **21**(4), 393-467.

Walther, F. R. (1965). Verhaltensstudien an der Grantgazelle (*Gazella granti* Brooke, 1872) im Ngorongoro-Krater. *Zeitschrift für Tierpsychologie*, **22**(2), 167-208.

Walther, F. R. (1978). Behavioral observations on oryx antelope (*Oryx beisa*) invading Serengeti National Park, Tanzania. *Journal of Mammalogy*, **59**(2), 243-260.

Walther, F. R., Mungall, E. C., & Grau, G. A. (1983). *Gazelles and their relatives: a study in territorial behavior*. William Andrew Publishing.

Warren, R. J., Vogelsang, R. W., Kirkpatrick, R. L., & Scanlon, P. F. (1978). Reproductive behaviour of captive white-tailed deer. *Animal Behaviour*, **26**, 179-183.

Weinberg, P. J. (2002). Capra cylindricornis. *Mammalian Species*, **695**, 1-9.

Williamson, D. T. (1994). Social behaviour and organization of red lechwe in the Linyanti Swamp. *African Journal of Ecology*, **32**(2), 130-141.

Wilson, P. (1984). Aspects of reproductive behaviour of bharal (*Pseudois nayaur*) in Nepal. *Zeitschrift für Säugetierkunde*, **49**(1), 36-42.

Wilson, V. J. (2001). *Duikers of Africa: masters of the African forest floor*. Zimbi books.

Yom-Tov, Y., Mendelssohn, H., & Groves, C. P. (1995). Gazella dorcas. *Mammalian Species*, **491**, 1-6.

CHAPTER 4: CO-OPTION OF ALARM SNORTS AS ALERTING SIGNALS IN THE ROARING DISPLAY OF MALE IMPALA ANTELOPES

ABSTRACT

In some ungulates and primates, males often give alarm calls at the beginning of complex agonistic vocalizations. Although such behaviour is relatively well documented, its adaptive value remains unknown. Here I investigated the evolutionary basis for alarm calling as part of the territorial roaring display of male impala antelopes (*Aepyceros melampus*). The roaring display consists of guttural grunting utterances, preceded by one or more "advertisement" snorts that sound indistinguishable from the alarm snorts emitted upon detecting predators. Using playback experiments, I therefore aimed at deciphering the information content of snorts and grunts in isolation, and of their combinations into roaring displays.

I found that male impala reacted with similar risk-aversive responses to playbacks of both alarm and advertisement snorts, i.e. retreating from the sound source. The two snorts also shared a similar acoustic structure, suggesting they were likely the same calls used in different contexts. Playbacks of both grunts in isolation and roaring displays (snorts + grunts) on the other hand elicited aggressive behaviour (i.e. approaching the sound source and vocalizing), consistent with a territorial signalling role. However, the presence of snorts in roaring displays significantly reduced the latency of an approaching reaction to the following grunts. I propose that the snort, which has its evolutionary origin as an alarm call, has been co-opted into the roaring display as an "alerting element", possibly increasing the salience of the grunting component, and thereby enhancing the effectiveness of information transfer. My findings indicate that alarm calls are used in the agonistic signalling systems of terrestrial mammals owing to efficacy-based selection pressure, which could therefore act as promoters of vocal complexity.

4.1 INTRODUCTION

Complex vocal displays, consisting of sequences of multiple acoustic elements, characterize male agonistic interactions in a variety of taxonomic groups: well-known examples include the “songs” of birds, whales, and some primates (Cowlishaw 1996; Marler & Slabbekoorn 2004; Clarke, Reichard & Zuberbuhler 2006; Gamba et al. 2016; Herman 2017; Searcy & Nowicki 2019; Garland & McGregor 2020). A vast amount of empirical and theoretical research has been devoted to understand the evolutionary origins and drivers of such elaborate vocalizations (e.g. Searcy & Anderson 1986; Catchpole 1987; Read & Weary 1992; Gil & Gahr 2002; Bolhuis, Okanoya, & Scharff 2010; Soma & Garamszegi 2011; Hill et al. 2018; Kareklas et al. 2019). However, it remains unclear whether or not songs and other multi-component vocal displays could derive from the combination of pre-existing calls, that have a different purpose when emitted in isolation (Collier et al. 2014; Manser et al. 2014; Manser 2016; Zuberbuhler & Lemasson 2014; Engesser & Townsend 2019). Available evidence suggests that this is usually not the case, as single components of aggressive utterances only acquire signal value when arranged into ordered strings (Marler & Mitani 1989; Berwick et al. 2012; Berwick & Chomsky 2013; Sainburg et al. 2019; Engesser & Townsend 2019). One possible exception may be represented by the “alarm-like” introductory notes in the loud agonistic vocalizations of several ungulates and monkeys (Marler 1972; Reby & McComb 2003; Passilongo et al. 2013; Schlenker et al. 2017). Are these equivalent to the alarm calls emitted during encounters with predators? And if so, what is their function in the agonistic context? In this study, I aimed at answering these questions by deciphering the information content of the roaring display of male impala antelopes (*Aepyceros melampus*).

The roaring display is an intra-sexual signal of territorial advertisement, and consists of an explosive nasal snort, or a series of snorts, followed by guttural grunting calls (Jarman 1979; Kingdon 1982; Frey et al. 2020; **Fig. 1**). Although the grunts are almost exclusively associated with confrontations over territory ownership (Jarman 1979; Murray 1982; Oliver, Skinner & Van der Merwe 2007; Frey et al. 2020), the “advertisement” snorts in the display exhibit surprisingly similar acoustic features to the alarm snorts elicited by the detection of an approaching predator (Caro 1994; Palmer & Gross 2018; Frey et al. 2020). The commonly accepted interpretation is that the alarm and advertisement snorts are the same calls, used in two different contexts (Jarman 1979; Kingdon 1982). This is however puzzling, as it could lead to an erosion of the original alarm message of the snorts, and undermine the reliability of the impala antipredator signalling system (Magrath et al. 2015; Mokkonen & Lindstedt 2016). In the face of such costs, snorting as part of roaring displays should thus provide substantial selective benefits to signallers.

Given their association with predation risk, alarm calls in agonistic vocal displays could prove advantageous to signallers by manipulatively inciting fearful reactions in competitors (*Manipulative Signal hypothesis*; Semple & McComb 1996; Wheeler 2009). A deceptive use of antipredator signals during conflicts has been widely documented among terrestrial vertebrates. For example, various birds and primates utter “false” alarm calls (i.e. in the absence of realized danger) to scare off conspecifics from foraging grounds and appropriate food items (in primates: Cheney & Seyfarth 1985; Wheeler 2009; in birds: Munn 1986; Flower, Gribble & Ridley 2014). A similar strategy is adopted by subordinate male chimpanzees (*Pan troglodytes*) in order to disrupt the courtship behaviour of dominant individuals, and gain access to oestrous females (de Waal 1986; Miles 1986). It is thus conceivable that snorting in the impala roaring display might as well reflect an attempt to deceive rivals into believing that a predator has been spotted, and discourage them from trespassing into occupied territories (regarded as dangerous). This could prevent the escalation of signalling contests into costly fights, and even prolong the duration of territorial tenure, with potentially positive effects on individual reproductive success (Murray 1982; Oliver et al. 2007).

Another possibility is that alarm calls have become co-opted into complex agonistic vocalizations as alerting elements (*Alerting Signal hypothesis*; Hebets & Papaj 2005; Partan & Marler 2005; Bro-Jørgensen 2010; Wiley 2013). An “alert” draws the attention of the receivers to the delivery of another signal that follows, thereby facilitating the detection and/or recognition of the latter, and ultimately reducing reaction times (Guilford &

Dawkins 1991; Ord & Stamps 2002; Hebets 2004; Hebets & Papaj 2005; Grafe & Wagner 2007; Bradbury & Vehrencamp 2011; Wiley 2013). Since alarm calls are both highly salient and pre-adapted for attention-grabbing (e.g. Manser 2001; Volodina et al. 2018), they might be ideally suited as alerts. The snorts of male impala are no exception, due to their perceived connection with imminent danger, and to their noisy acoustic structure (i.e. lack of harmonics), broad bandwidth, and abrupt onsets and offsets (Frey et al. 2020): all properties known to be particularly evocative to listeners (Morton 1977; Fitch, Neubauer & Herzel 2002; Reby & Charlton 2012). Hence, snorting at the beginning of a roaring display might assist receivers in concentrating on the relevant agonistic information broadcasted by the following grunting calls. In the relatively dense vegetation of impala breeding territories, where the opportunity for visual communication between competitors is limited (Owen-Smith 1977; Jarman 1979), this would ensure that the threat posed by vocalizing rivals is promptly evaluated and dealt with.

Here I tested the validity of the adaptive hypotheses discussed above (Manipulative Signal, Alerting Signal), by exposing male impala to playbacks of (i) snorts and grunts in isolation, and (ii) their combinations into roaring displays (cf. Partan & Marler 2005). I first investigated whether the advertisement snorts in the roaring display were indeed indistinguishable from the alarm snorts. Accordingly, I expected the two types of snorts to have similar acoustic structure, and to both evoke retreats from the sound source during playbacks, in line with a putative alarm role (cf. Bro-Jørgensen & Pangle 2010). I then proceeded to investigate the message contained in grunts and roaring displays (snorts + grunts). Since grunting calls are exclusively emitted during sexual-aggressive interactions, I predicted that, contrary to snorts, they would provoke approaching and vocalizing behaviours typical of territorial disputes (Jarman 1979; Murray 1982). On the other hand, the responses to roaring displays were expected to vary depending on the main function of the snorting component: (i)Under the Manipulative Signal hypothesis, I predicted that male impala would associate the snorts in the roaring displays with imminent danger, and thus be less likely to approach playbacks of roaring displays than playbacks of grunts in isolation. This should be especially evident with roaring displays containing a very large number of snorts (snort-dominated displays from now onwards), which may denote a high-risk situation (Caro 1994; Meise, Franks & Bro-Jørgensen2018). Under the Alerting Signal hypothesis, I conversely predicted that snorting in roaring displays would not modify the aggressive message of the grunting calls, but instead increase their salience. Hence, I expected that male impala presented with playbacks of roaring displays would start approaching the sound source at a shorter latency than those exposed to grunts in isolation. Hypotheses and predictions are summarized in **Table 1**.

4.2 METHODS

Study system

The study was conducted in the Maasai Mara National Reserve, a protected area in south-western Kenya which covers varied landscapes ranging from open grasslands to dense thickets. The Mara is characterized by bimodal rainfall patterns, with peaks in November-December and March-May. Male impala in the Serengeti-Mara ecosystem maintain breeding territories and are vocally active for most of the year, except during the driest months (June-August; Schenkel 1966; Jarman 1979; Ogutu et al. 2015). Territories are defended against intruding adult males and contain relevant forage resources that attract female herds (Jarman 1979; Murray 1982).

Impala of both sexes snort when detecting ambush predators (in the study area: lion *Panthera leo*, leopard *Panthera pardus*, cheetah *Acinonyx jubatus*, and humans; Estes 1991; Meise et al. 2018), assuming a typical alert posture, with neck erected and ears pricked. By contrast, roaring displays are almost exclusively emitted by adult males that have attained territory ownership (Jarman 1979; Murray 1982; Oliver et al. 2007). Territorial males roar spontaneously, when chasing and confronting intruding males, and even during herding of females (although the latter do not seemingly pay attention to the display, which is primarily directed at same-sex competitors; Schenkel 1966; Jarman 1979; G. D'Ammando, pers. obs.). The male posture during roaring is characterized by a forward-stretched neck, lifted muzzle and tail gradually raised to about 45 degrees, often during fast walking or running (**Fig. 2**; Leuthold 1977; Jarman 1979).

Stimulus acquisition

Roaring displays were recorded at a distance of 35-40 m using a directional microphone (Sennheiser ME67) connected to a digital audio recorder (Marantz PMD670). Roaring was incited by broadcasting an unaltered recording of a roaring display (duration = 3.870 s; recorded by J. Bro-Jørgensen) to 25 territorial male impala, using a loudspeaker (Mipro MA707) positioned at ground level and connected to a digital audio recorder (Tascam H2-P2). Vocalizations were surveyed in Praat v. 6.0.3 (Boersma & Weenink 2017), and high-quality exemplars (i.e. with no overlapping sounds) from eight different individuals were selected for the construction of playback stimuli. Recordings of alarm snorts were obtained, using the same equipment, by presenting territorial male impala (n = 10) with a cardboard model of a leopard (based on a high-resolution photo), placed at 50-80 m and at a ~90° angle from the focal animal. Four high-quality recordings were chosen for further playback experiments.

Acoustic analyses

I analysed the duration and peak frequency of alarm and advertisement snorts in Praat (Boersma & Weenink 2017). I focused on 28 different male impala (including additional recordings from this study, and from a previous research project on the same population; Meise et al. 2018), and examined an average of 1.607 ± 0.139 (range 1-4) snorts per individual. Snort duration was measured in narrow-band spectrograms generated by fast Fourier transformation (Gaussian window length=0.025 s; time steps=1000; frequency steps=2500). Peak frequency was considered as the frequency of greatest energy observed on a power spectrum after cepstral smoothing at 1000 Hz.

Construction of playback stimuli

All recorded exemplars were edited in Audacity 2.1.0 (Audacity Team 2017) in order to obtain four types of playback stimuli: (i) snorts (alarm or advertisement); (ii) grunts; (iii) snort-dominated roaring displays (10 snorts + 1 grunt); and (iv) grunt-dominated roaring displays (1 snort + 1 grunt; defined as "grunt-dominated" given the considerably longer duration of the grunting component). I manipulated the number of snorts (1 or 10), and the number of syllables in the grunts (2, 4, or 16), in order to reflect natural variation in call duration (Appendix I). All stimuli were standardized to natural amplitudes (60-63 dB), measured in the field at a distance of 35 m with the aid of a sound level meter (UNI-T, Model UT352).

Playback experiments

I conducted 222 playback trials on territorial male impala, in an attempt for a balanced design (mean ± SE = 55.5 ± 3.5 trials per stimulus type). Stimuli were presented to both solitary (n=114) and harem-holding males (n=108), following a randomized order. Each exemplar was never broadcasted more than five times (mean ± SE = 3.763 ± 0.183 trials per exemplar). To prevent double-sampling, I identified individual male impala by reporting distinctive morphological traits (horn shape and ridges, ear notches, albinisms, and scars; Jarman 1979) on custom-made identity cards, and avoided conducting trials on animals which had been previously targeted. Moreover, I travelled > 800 m between playback sites on the same day (beyond the active space of impala vocalizations; G. D'Ammando, pers. obs.), and played back stimuli at distances greater than the maximum estimated diameter of impala territories (~ 250 m; Jarman 1979) on different days. The risk for pseudo-replication to affect the results was therefore minimal. The territorial status of male impala was inferred from behavioural cues observed over a period of ≥ 10 minutes before the start of each playback trial (Appendix II).

Stimuli were presented to stationary, foraging individuals after 20 seconds of uninterrupted grazing. All responses were recorded on a digital video camera (Sony HDR-PJ810E). Filming was ended once the focal animal had returned to grazing for at least 10 seconds, or moved out of view. Trials were only conducted in conditions of low wind speed (≤ 3.0 m/s), measured with an anemometer (Proster Digital LCD); and at a distance of 45-80 m, measured with a laser rangefinder (Bushnell Scout DX 1000 ARC). Grass height and distance to woody vegetation cover at playback sites were visually estimated by comparison with the body height and length of an adult male impala (measurements taken from Estes 1991; and Kingdon 2015). For harem-holding males, I also counted the number of adult females (> 3 years old, with a visible udder; Averbeck et al. 2010) forming the harem, using 8x42 Nikon Aculon binoculars. Playback procedure is summarized in **Fig. 3**.

Behavioural analyses

Video recordings of playback trials were processed in BORIS (Behavioural Observation Interface Software; Friard & Gamba 2016) using frame-by-frame analyses (temporal window length = 0.04 s). Behavioural responses occurring within 2 minutes from stimulus presentation were categorically classified as: (i) approaching the speaker; (ii) retreating from the speaker and (iii) vocalizing (only roaring displays, as snorts and grunts in isolation occurred very infrequently: n = 6). I conservatively considered as genuine approaches or retreats only movements of ≥ 10 steps in an uninterrupted walking bout. This ensured that small-scale orienting behaviour was excluded from analyses. The latency to approach the speaker was calculated, for the playbacks of grunts and roaring displays that elicited this response (n = 97), as the time interval from grunting onset (measured on a BORIS spectrogram) at which the first movement of the front legs of a focal individual could be observed. Impala in the study population did not react to control bird sounds (ring-necked dove *Streptopelia capicola*) in a previous study which adopted a similar playback design (Meise et al. 2018). I could therefore be reasonably sure that observed responses were not an artefact of my experimental setting.

Statistical analyses

All statistical analyses were conducted in R 3.5.2 (R Development Core Team 2019). The duration and peak frequency of alarm and advertisement snorts were compared using Wilcoxon rank-sum tests. Differences in the response frequencies (approach, retreat, or vocalize) to playbacks of the two type of snorts, on the other hand, were estimated using chi-square tests of independence. Multivariate analyses did not show any significant effects of socio-ecological variables (i.e. distance to focal individual, grass height, etc.) on the reactions of male impala to alarm and advertisement snorts, and the results are thus not reported here.

The probabilities of retreating, approaching, and vocalizing in response to playbacks of snorts, grunts, and roaring displays were modelled as binary response variables in Generalized Linear Mixed Models (GLMMs) with binomial error distribution and logit link function (McCullouch & Neuhaus 2003). Separate models were fitted to each of the three different behavioural responses. Latency to approach the speaker was re-scaled to milliseconds in order to obtain integer values, and entered as a response variable in GLMMs with zero-truncated negative binomial error distribution (Zuur et al. 2009; Yau et al. 2013). This method has been successfully employed to analyse highly skewed "time-to" data in previous studies (e.g. Duffield, Wilson & Thornton 2015), and was preferred over survival analysis due to the violation of residual proportionality assumptions in my dataset (Kutner, Nachtsheim & Neter 2005). Fixed effect explanatory variables in all models included the type of the playback stimulus (snorts, grunts, snort-dominated roaring display, and grunt-dominated roaring display), and the following socio-ecological variables: male status (solitary or harem-holding); distance from the speaker; wind speed; proximity to cover; and grass height. Harem size was converted from continuous to categorical ("male status") in order to resolve multiple convergence warnings in model fit (Allison 2004). All continuous explanatory variables were log-transformed to make them suitable for analyses. Stimulus duration (as defined by the number of snorts and of syllables in the grunts; Appendix I), and stimulus identity were entered in the models as random effects, in order to control for noise generated by variability among exemplars. All modelling was performed in the glmmTMB package (Magnusson et al. 2019).

Model selection was implemented via progressive removal of predictors in order of least significance ($p > 0.05$; Murtaugh 2014). Multicollinearity between explanatory variables was checked by calculating Variance Inflation Factors (VIFs). All VIFs were ≤ 2.09, thus well below the accepted threshold of concern of 5-10 (Kutner et al. 2005). In negative binomial GLMMs, the theta parameter was not significantly different from 1 ($\theta = 0.86 – 1.35$), thereby excluding the risk of residual over-dispersion. The statistical significance of post-hoc contrasts for categorical variables was calculated by applying The Hollman-Bonferroni correction in the lsmeans package (Lenth & Lenth 2018).

4.3 RESULTS

Differences between alarm and advertisement snorts

I did not find any detectable differences between advertisement and alarm snorts, neither in peak frequency (1716 ± 127 Hz; Mann-Whitney U = 268.5; n_1 = 22 alarm snorts, n_2 = 25 advertisement snorts; P=0.932), nor in duration (293 ± 12 ms; Mann-Whitney U = 344.5; n_1 = 22 alarm snorts, n_2 = 25 advertisement snorts; P =0.129; **Fig. 4**). Furthermore, the two types of snorts elicited similar responses during playbacks (approaching: $\chi^2 = 0.002$, df = 1, P = 0.963; retreating: $\chi^2 = 0.046$, df = 1, P = 0.831; vocalizing: $\chi^2 = 0.002$, df = 1, P = 0.963; n_1 = 19 alarm snorts, n_2 = 20 advertisement snorts), with retreats from the speaker observed in the majority of trials (68 %; **Fig. 5**). This implies that all snorts in isolation conveyed equivalent messages, and were likely perceived as alarm calls irrespectively of the original context of production.

Information content of snorts, grunts, and roaring displays

Playbacks of snorts in isolation evoked retreating behaviour in territorial male impala significantly more often than playbacks of grunts (log-odds ratio = 1.587 ± 0.408: t = 3.888; P < 0.001; **Table 2**; **Fig. 6**), consistent with an alarm function. By contrast, playbacks of grunts were more likely than snorts to cause territorial male impala to approach the speaker (log-odds ratio = 2.903 ± 0.693: t = 4.189; P < 0.001; **Table 3**; **Fig. 6**), and to vocalize (log-odds ratio = 2.579 ± 0.887: t = 2.906; P = 0.021; **Table 4**; **Fig. 6**). This is consistent with these calls primarily encoding agonistic information. Playbacks of roaring displays (snorts + grunts) also provoked aggressive behaviour (i.e. approaching and vocalizing) more frequently than snorts (**Table 3** & **Table 4**; **Fig. 6**). However, contrary to the expectations of the Manipulative Signal hypothesis, focal individuals were not less likely to approach the speaker in response to roaring displays than in response to grunts (grunt-dominated displays versus grunts: log-odds = 0.234 ± 0.565; t = 0.414; P = 0.976), not even when roaring displays contained a large number of snorts (snort-dominated displays versus grunts: log-odds = 0.021 ± 0.580; t = -0.036; P = 1.000; **Fig. 6**). Conversely, male impala approached the speaker with significantly shorter latency after hearing both grunt-dominated (latency mean ± SE = 10.458 ± 2.745 s; b = -0.915 ± 0.329; t = -2.778; P = 0.018) and snort-dominated roaring displays (mean ± SE = 7.512 ± 3.225; b = 1.45 ± 0.466; t = 3.116; P = 0.007) than when hearing grunts in isolation (mean ± SE = 21.694 ± 3.581; grunt-dominated vs grunts = -0.915 ± 0.329; t = -2.778; P = 0.018; **Fig. 7**). These response patterns support the Alerting Signal hypothesis.

4.4 DISCUSSION

I found that the advertisement snorts in the roaring display of territorial male impala were indistinguishable from the alarm snorts emitted upon detecting predators. The two types of snorts had similar acoustic structure, and elicited similar risk-aversive behaviour (i.e. retreating from the sound source) during playback trials. Nonetheless, snorts did not evoke retreats when combined with grunting calls into roaring displays. By contrast, their presence significantly reduced the latency of an aggressive response (i.e. approaching the sound source) to the following grunts. This suggests that the snort, with its evolutionary origin as an alarm call, has been co-opted for a secondary, derived function as an alerting element in the roaring display.

The results confirm that the roaring display is a combination of two pre-existing calls, snorts and grunts, which are meaningful in isolation, and contain different, non-overlapping information. In particular, snorts in isolation are seemingly perceived as notifications of predation risk (cf. Bro-Jørgensen & Pangle 2010; Palmer & Gross 2018; Meise et al. 2018). On the other hand, the approaching and vocalizing behaviours incited by playbacks of grunts in isolation are consistent with aggressive signalling during territorial disputes (Jarman 1979; Oliver et al. 2007). In this respect, grunts may be functionally equivalent to the loud agonistic vocalizations of other ungulates, and, pending further investigations, also encode relevant cues to individual competitive ability (e.g. body size, stamina; cf. red deer *Cervus elaphus* Reby et al. 2005, Charlton & Reby 2016; fallow deer *Dama dama* Vannoni & McElligott 2008; and goitered gazelle *Gazella subgutturosa* Blank, Ruckhstul & Yang 2014). However, if grunting on its own is sufficient to convey an unambiguous agonistic message, what is the value of snorts in the roaring display?

In playback trials, snorts combined with grunts did not substantially alter the message content of the latter, as evidenced by the qualitatively similar responses of male impala (i.e. approaching and vocalizing) to both grunts in isolation and roaring displays (snorts + grunts). Nevertheless, focal individuals usually moved towards playbacks of grunts only long after the stimulus had ended. To the contrary, those presented with roaring displays often started an approach immediately after the grunting component of the stimulus had been broadcasted. Therefore, the introductory snorting phase appeared to lower the threshold for an appropriate reaction to the subsequent grunts, in agreement with alerting signal theory (Guilford & Dawkins 1991; Hebets & Papaj 2005; Wiley 2013). I propose that the snorts might have a “priming effect” on receivers (Hebets & Papaj 2005; Bradbury & Vehrencamp 2011), by making them aware to the possibility that a grunting call may follow. This would decrease the time required for discriminating and processing the agonistic information contained in the grunts, and improve the overall effectiveness of the display.

A striking parallel can be drawn with the territorial song of the rufous-headed towhee (*Pipilo erythrophthalmus*). In this North American bird, males also react earlier, with aggressions and vocalizations, to singing bouts introduced by an alerting “trill” (Richards 1981). Shorter response latencies to agonistic signals preceded by alerts have also been documented in other birds (Nelson 2017), and even in the gestural displays of male *Anolis* lizards (Ord & Stamps 2008). The snorts of male impala are anyway unique among alerting elements, in the primary role of alarm calls. Since the impala has a small and rather fixed vocal repertoire (only four different vocalizations described to date; Jarman 1979; Frey et al. 2020), selection for signal efficacy may have favoured the integration of the snort, a highly salient vocalizaton shaped to get attention, over the evolution of an entirely novel component (cf. Gould & Vrba 1974).

With regard to the exact alerting mechanism of the snorts, I can only advance speculative explanations. One possibility is that the harshness and chaotic acoustics of these utterances could promote selective attention in receivers, and hence speed up the recognition of the grunting calls transmitted on the same sensory channel (Guilford & Dawkins 1991; Hebets & Papaj 2005; Hebets et al. 2016). Supporting this interpretation, harsh sounds have been demonstrated to generate heightened responsiveness in different lineages of mammals (humans included; Slocombe & Zuberbuhler 2007; Townsend & Manser 2011; Reby & Charlton 2012). Alternatively, the close link between snorts and imminent danger could increase fear-mediated testosterone production, and thus induce arousal and, subsequently, increased reactivity to external stimuli (Gyger et al. 1988; Blumstein & Recapet 2009; Fedurek et al. 2016). At the moment, the respective impacts of snort design and information content on the salience of the roaring display remain difficult to tell apart. This issue might be solved through re-synthesis techniques, which allow for controlling variation on different acoustic parameters; and by monitoring the hormonal changes of impala exposed to different call types.

A potential problem arising from the double use of snorts as both alarm calls and alerting display elements, is that it might confuse their interpretation by receivers, with deleterious consequences on individual survival and/or reproductive success (Schlenker, Chemla & Zuberbuhler 2016; Dezecache & Berthet 2018). My playback experiment showed that, in some instances, focal individuals reacted aggressively to snorts in isolation – a costly decision in the presence of an actual predator (Sherman 1985; Bergstrom & Lachmann 2001). At the same time, the introductory snorts in roaring displays occasionally triggered retreats, which could be disadvantageous during confrontations with intruders (i.e. due to the higher chance of losing territory ownership; Maynard-Smith 1979; Krebs 1982). Such errors were however very rare, and, in most cases, male impala appeared able to discern that snorts followed by grunts were not to be interpreted as alarm calls, and vice versa. Grunting thus appears to operate as a "contextual modifier" (cf. Ouattara et al. 2009; Berthet et al. 2019; Engesser & Townsend 2019), with its presence or absence helping receivers in retrieving the exact context of snort production (advertisement or alarm, respectively), and reducing the inherent ambiguity associated with snorting.

Surprisingly, the large number of snorts in snort-dominated roaring displays did not further reduce impala response latencies, when compared to a single snort (i.e. in grunt-dominated displays). Since the production of fast snort sequences (up to 13; Appendix I) might be costly in energetic terms, this demands evidence of communication benefits. A tentative explanation could be that the repetitions serve as backup signals to increase display redundancy and thus favour detection by receivers (Johnstone 1996; Brumm & Slater 2006; Hebets et al. 2016).

My findings delineate a possible adaptive path for the inclusion of alarm calls as part of mammalian aggressive displays. A comparative approach would be helpful in determining whether or not the alerting signal hypothesis could also explain the convergent adaptations to male impala observed across other species. These include, but are by no means restricted to, the alarm barks introducing the roars of red deer (Reby & McComb 2003; Passilongo et al. 2013), and the alarm-like components incorporated in the loud territorial utterances of various forest primates (e.g. black-and-white colobus monkey *Colobus guereza* Marler 1972; gibbons *Hylobates* sp. Mitani 1985; indri lemur *Indri indri* Giacoma et al. 2010; howler monkeys *Alouatta* ssp. Kitchen et al. 2015).

In mammals, the evolution of complex vocalizations has usually been attributed to sexual selection (Cowlishaw 1996; Gustison & Bergman 2016), or to the need for a greater variety of social signals in large groups (cf. the "social complexity hypothesis"; McComb & Semple 2005; Freeberg, Dunbar & Ord 2012; Gustison, Le Roux & Bergman 2012; Bouchet, Blois-Heulin, & Lemasson 2013; Manser 2016; Dunn & Smaers 2018). Here I show that call combinations can also emerge under efficacy-based selection pressures in agonistic contexts. Future studies should therefore take into account the potential for multiple evolutionary forces to generate complexity by analysing vocal repertoires as the building blocks of signal elaboration and diversification.

4.5 CONCLUSION

This study provides experimental evidence that the alarm snort of male impala antelopes has been co-opted into the roaring display of territorial advertisement for an alerting function. Specifically, I observed that snorting reduces the response latency of the receivers to the agonistic message encoded in the grunting component of the display, and thus seemingly enhances efficacy of this communication system. Additional research is now necessary to test the applicability of my alerting signal interpretation at a broader taxonomic scale.

4.6 TABLES

Table 1: Summary of the hypotheses proposed to explain the function and information content of the different call components of the roaring display of territorial male impala.

	Predicted responses		
Hypotheses	Snort	Grunt	Roaring display (Snort + Grunt)
Manipulative signal	 +	 =	
Alerting signal	 +	 =	

= Retreat

= Approach and/or display

Table 2: GLM model of the probability of male impala retreating from the speaker during playback experiments as a binary (1/0) response variable. The reference level for the playback stimulus predictor is the "grunt – dominated" (i.e. one snort + grunting) roaring display.

	Coefficient	S.E.	t	P
Stimulus - *Grunt*	0.251	0.427	0.588	0.557
Stimulus – *Snort-dominated roaring display*	0.028	0.470	0.059	0.953
Stimulus - *Snort*	1.838	0.421	4.361	**<0.001**
Male - *Solitary*	-0.573	0.312	-1.836	*0.066*
Distance (log)	1.435	0.982	1.462	0.144
Grass Height (log)	0.168	0.189	0.889	0.374
Cover (log)	0.136	0.097	1.462	0.161
Log(Wind Speed)	0.783	0.321	2.438	**0.015**

Table 3: GLM model of the probability of male impala approaching the speaker during playback experiments as a binary (1/0) response variable.

	Coefficient	S.E.	t	P
Stimulus - *Grunt*	-0.234	0.565	-0.414	0.679
Stimulus – *Snort-dominated roaring display*	-0.213	0.584	-0.365	0.715
Stimulus - *Snort*	-3.137	0.699	-4.488	**<0.001**
Male - *Solitary*	0.210	0.317	0.663	0.501
Distance (log)	-1.791	0.996	-1.797	*0.072*
Grass Height (log)	-0.173	0.196	-0.881	0.378
Cover (log)	0.084	0.098	0.848	0.396
Wind Speed (log)	-0.468	0.330	-1.416	0.157

Table 3: GLM model of the probability of male impala engaging into vocal displays during playback experiments as a binary (1/0) response variable.

	Coefficient	S.E.	t	P
Stimulus - *Grunt*	-0.1154	0.839	-0.136	0.892
Stimulus – *Snort-dominated roaring display*	0.396	0.874	0.452	0.651
Stimulus - *Snort*	-2.693	0.880	-3.060	**0.002**
Male - *Solitary*	0.053	0.354	0.149	0.882
Distance (log)	-0.620	1.101	-0.564	0.573
Grass Height (log)	-0.438	0.222	-1.979	**0.048**
Cover (log)	0.037	0.108	0.345	0.730
Wind Speed (log)	-0.700	0.394	-1.779	*0.075*

Table 5: GLM zero-truncated negative binomial model of the latency of male impala to approach the speaker during playbacks as the response variable (n=97). Latency to approach was measured from the onset of the grunting call in all stimuli. The reference level for the playback stimulus is the grunt-dominated roaring display.

	Coefficient	S.E.	t	P
Stimulus - *Grunting*	1.083	0.418	2.592	**0.009**
Stimulus – *Snort-dominated roaring display*	-0.370	0.453	-0.818	0.413
Male - *Solitary*	0.645	0.268	2.594	**0.009**
Distance (log)	0.900	0.750	1.200	0.230
Grass Height (log)	0.556	0.172	3.225	**0.001**
Cover (log)	-0.064	0.072	0.892	0.372
Wind Speed (log)	0.102	0.299	0.342	0.732

4.7 FIGURES

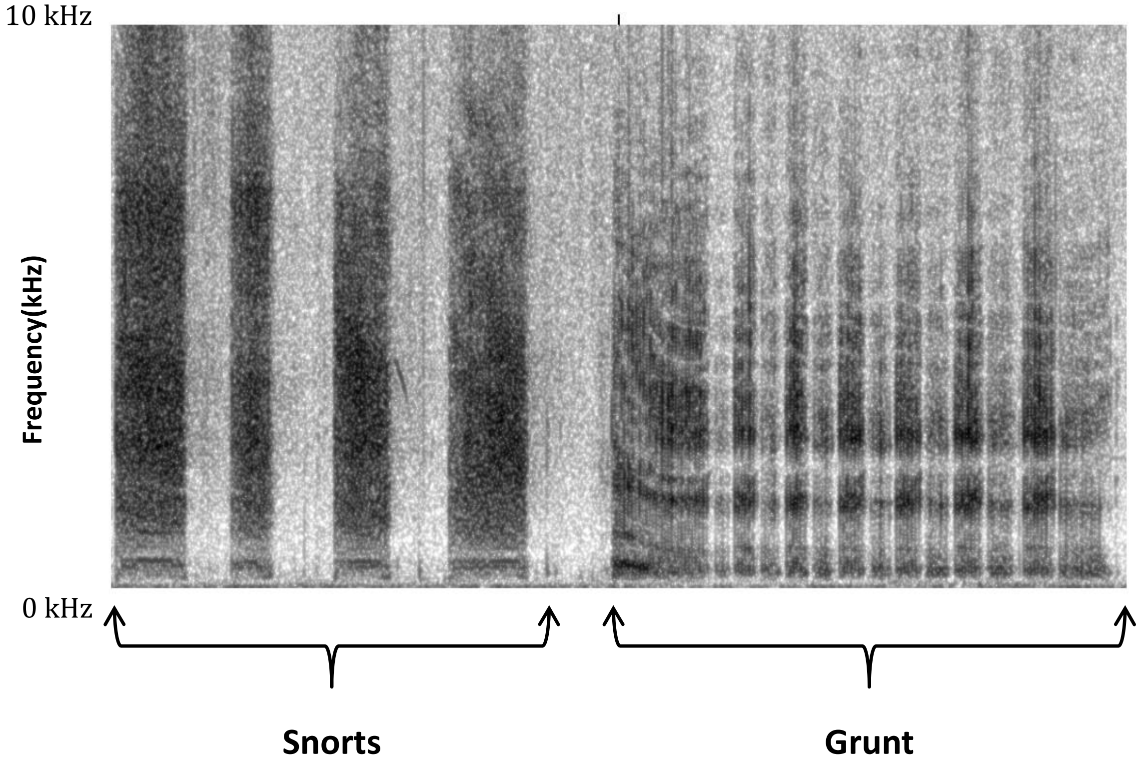


Figure 1: Narrow-band spectrogram of a male impala roaring display (Gaussian window length=0.025 s; time steps=1000; frequency steps=2500). This exemplar contains four snorts (left), followed by a multi-syllable grunting call (right).

Figure 2: Territorial male impala during a roaring display. The male is in the typical roaring posture, with stretched neck, lowered larynx (to mid-neck position), and raised, fanned tail. Picture by Claudio Graziani.

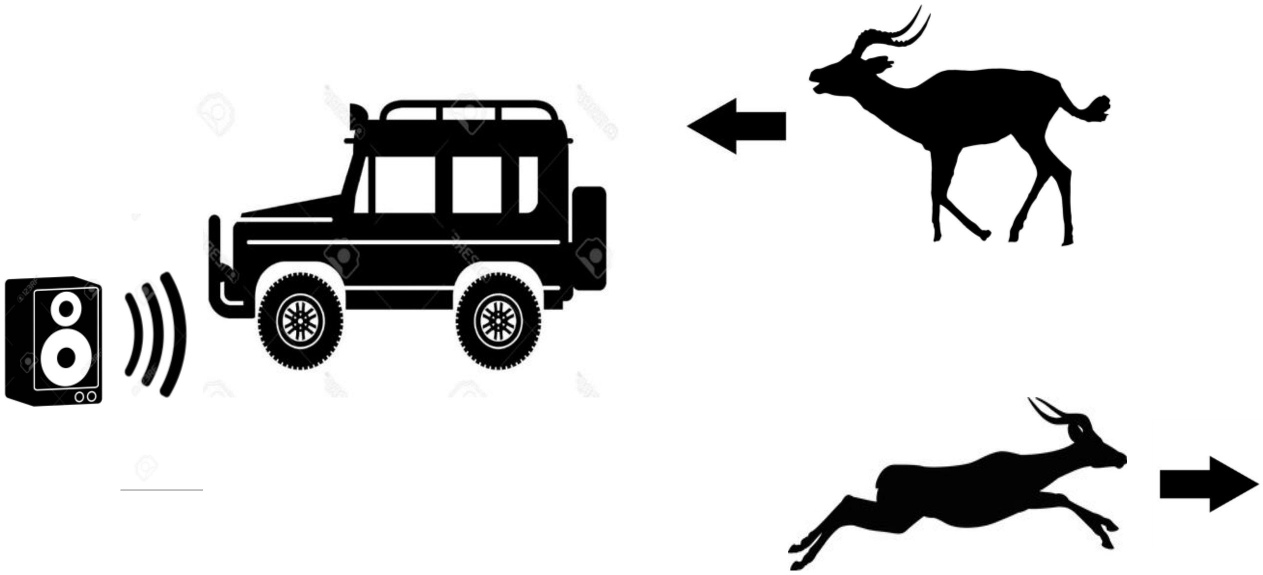


Figure 3: Playback experimental protocol. Movements of territorial male impala in reaction to playback stimuli were classified as either approaching to, or retreating from, a loudspeaker hidden by the car silhouette.

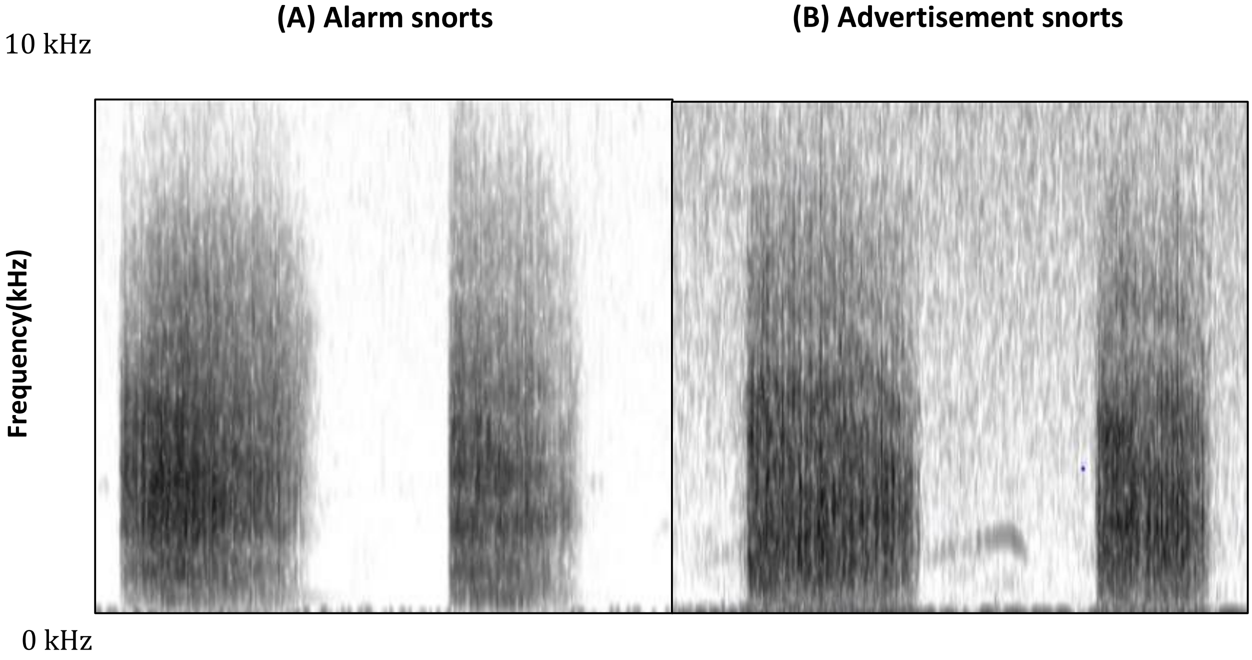


Figure 4: Narrow-band spectrograms of two male impala alarm snorts (A), and of two advertisement snorts extracted from a roaring display (B; Gaussian window length=0.025 s; time steps=1000; frequency steps=2500).

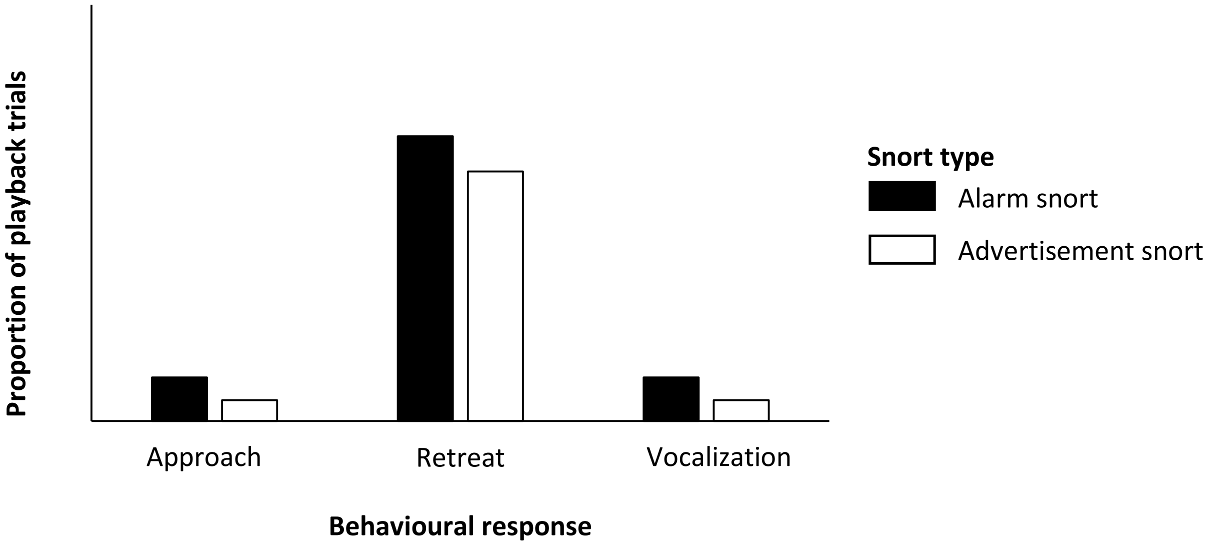


Figure 5: Responses to playbacks of alarm (n_1 = 19) and advertisement snorts (n_2 = 20).

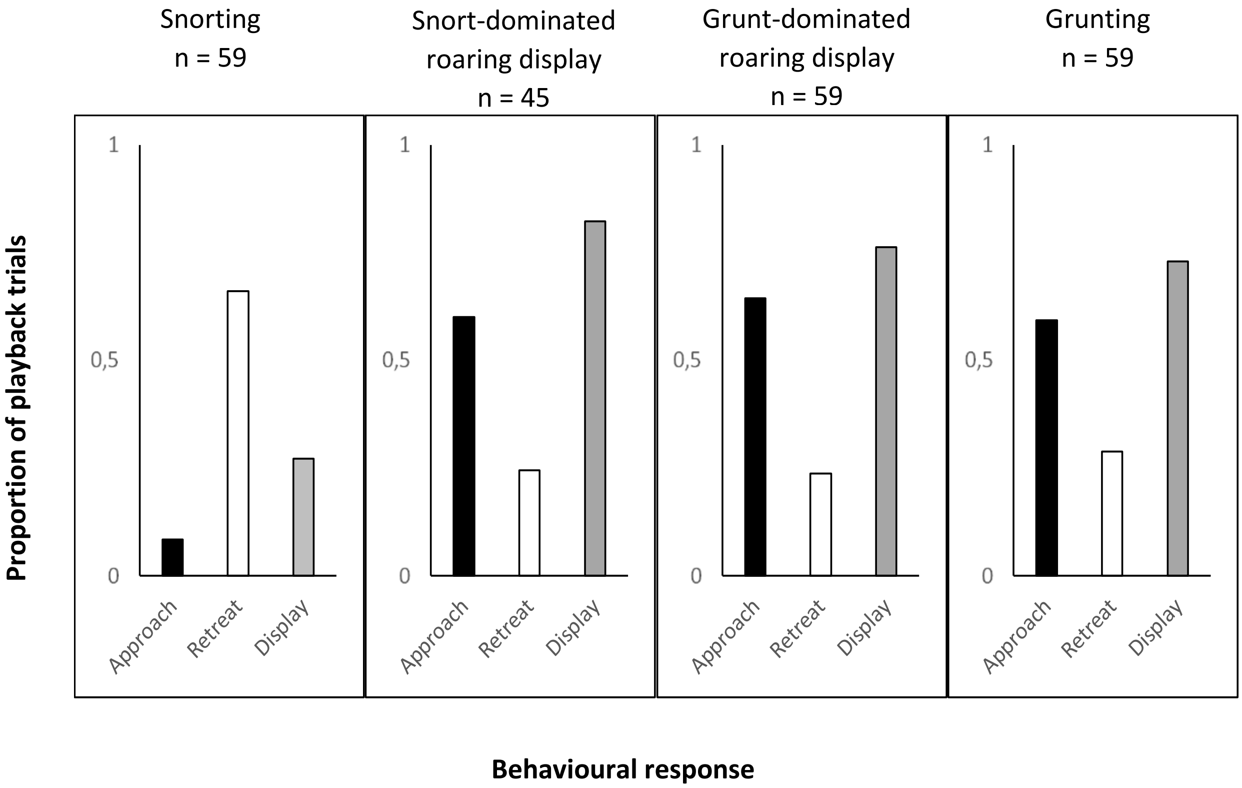


Figure 6: Proportion of trials eliciting approaches, retreats, or vocal displays in response to the four different playback stimulus types.

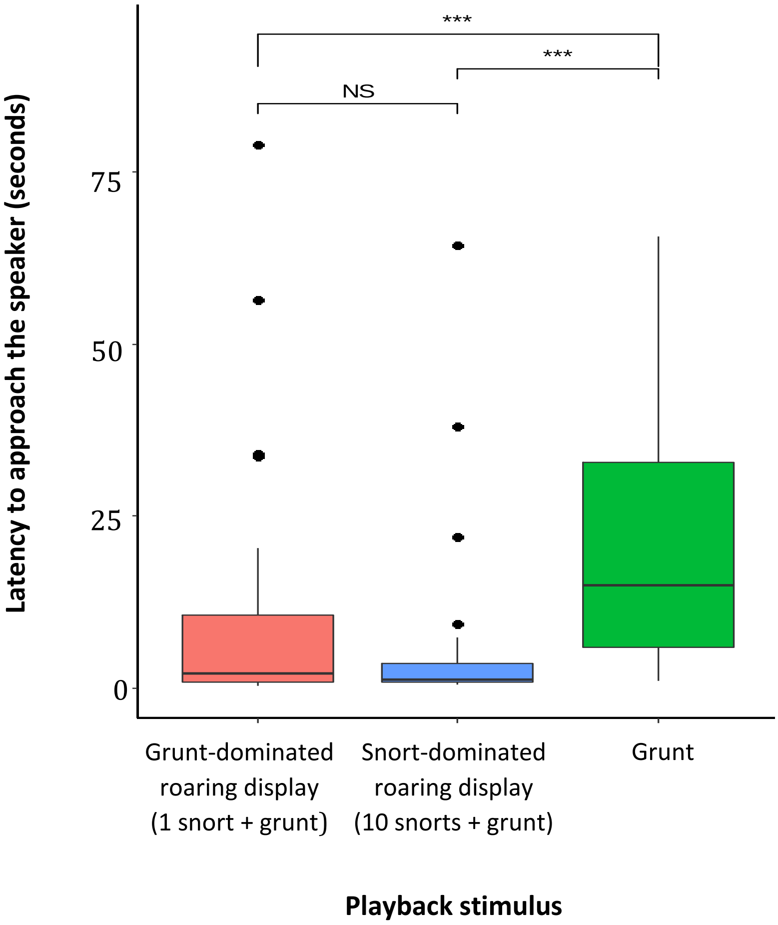


Figure 7: Latency (in seconds) to approach the speaker by territorial male impala in response to: (i) grunt-dominated roaring displays; (ii) snort-dominated roaring displays; and (iii) grunts in isolation. Latencies are calculated from the onset of the grunting component in roaring displays. Top horizontal bars indicate levels of statistical significance in multiple pairwise comparisons (*<0.05; **<0.01; ***<0.001; NS=Non-Significant).

4.8 REFERENCES

Allison, P. (2004). Convergence problems in logistic regression. *Numerical Issues in Statistical Computing for the Social Scientist*, 238-252.

Audacity Team (2017). *Audacity(R): Free Audio Editor and Recorder [Computer application]. Version 2.1.0*. https://audacityteam.org/

Averbeck, C., Apio, A., Plath, M., & Wronski, T. (2010). Hunting differentially affects mixed-sex and bachelor-herds in a gregarious ungulate, the impala (*Aepyceros melampus*: Bovidae). *African Journal of Ecology*, **48**(1), 255-264.

Bergstrom, C. T., & Lachmann, M. (2001). Alarm calls as costly signals of antipredator vigilance: the watchful babbler game. *Animal behaviour*, **61**(3), 535-543.

Berthet, M., Mesbahi, G., Pajot, A., Cäsar, C., Neumann, C., & Zuberbühler, K. (2019). Titi monkeys combine alarm calls to create probabilistic meaning. *Science Advances*, **5**(5), 3991.

Berwick, R., Beckers, G., Okanoya, K., & Bolhuis, J. (2012). A bird's eye view of human language evolution. *Frontiers in evolutionary neuroscience*, **4**, 5.

Berwick, R. C., & Chomsky, N. (2013). *Birdsong, speech, and language: exploring the evolution of mind and brain*. MIT press.

Blank, D. A., Ruckstuhl, K., & Yang, W. (2014). Roaring function in male goitered gazelles. *Behavioural Processes*, **106**, 152-159.

Blumstein, D. T., & Recapet, C. (2009). The sound of arousal: The addition of novel non-linearities increases responsiveness in marmot alarm calls. *Ethology*, **115**(11), 1074-1081.

Boersma, P. P. G., & Weenink, D. J. M. (2017). *Praat: Doing Phonetics by Computer: Version 6.0.3*. Instituut voor Fonetische Wetenschappen.

Bolhuis, J. J., Okanoya, K., & Scharff, C. (2010). Twitter evolution: converging mechanisms in birdsong and human speech. *Nature Reviews Neuroscience*, **11**(11), 747-759.

Bouchet, H., Blois-Heulin, C., & Lemasson, A. (2013). Social complexity parallels vocal complexity: a comparison of three non-human primate species. *Frontiers in Psychology*, **4**, 390.

Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication*. Sinauer.

Bro-Jørgensen, J. (2010). Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends in Ecology & Evolution*, **25**(5), 292-300.

Bro-Jørgensen, J., & Pangle, W. M. (2010). Male topi antelopes alarm snort deceptively to retain females for mating. *The American Naturalist*, **176**(1), 33-39.

Brumm, H., & Slater, P. J. (2006). Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behavioral Ecology and Sociobiology*, **60**(4), 475-481.

Caro, T. M. (1994). Ungulate antipredator behaviour: preliminary and comparative data from African bovids. *Behaviour*, **128**(4), 189-228.

Catchpole, C. K. (1987). Bird song, sexual selection and female choice. *Trends in Ecology & Evolution*, **2**(4), 94-97.

Charlton, B. D., & Reby, D. (2016). The evolution of acoustic size exaggeration in terrestrial mammals. *Nature Communications*, **7**(1), 1-8.

Cheney, D. L., & Seyfarth, R. M. (1985). Vervet monkey alarm calls: Manipulation through shared information? *Behaviour*, **94**(1), 150-166.

Clarke, E., Reichard, U. H., & Zuberbühler, K. (2006). The syntax and meaning of wild gibbon songs. *PloS One*, **1**(1), e73.

Collier, K., Bickel, B., van Schaik, C. P., Manser, M. B., & Townsend, S. W. (2014). Language evolution: syntax before phonology?. *Proceedings of the Royal Society B: Biological Sciences*, **281**(1788), 20140263.

Cowlishaw, G. U. Y. (1996). Sexual selection and information content in gibbon song bouts. *Ethology*, **102**(2), 272-284.

Dezecache, G., & Berthet, M. (2018). Working hypotheses on the meaning of general alarm calls. *Animal Behaviour*, **142**, 113-118.

De Waal, F. B. (1986). Deception in the natural communication of chimpanzees. In Mitchell, R. V., & Thomson, R. S. (Eds). *Deception: Perspectives on human and nonhuman deceit*, 221-244. Suny Press, Albany.

Duffield, C., Wilson, A. J., & Thornton, A. (2015). Desperate prawns: drivers of behavioural innovation vary across social contexts in rock pool crustaceans. *PLoS One*, **10**(10), e0139050.

Dunn, J. C., & Smaers, J. B. (2018). Neural Correlates of Vocal Repertoire in Primates. *Frontiers in Neuroscience*, **12**, 534.

Engesser, S., & Townsend, S. W. (2019). Combinatoriality in the vocal systems of nonhuman animals. *Wiley Interdisciplinary Reviews: Cognitive Science*, e1493.

Estes, R. D. (1991). *The Behaviour Guide to African Mammals*. University of California Press, Berkeley (USA).

Fedurek, P., Slocombe, K. E., Enigk, D. K., Thompson, M. E., Wrangham, R. W., & Muller, M. N. (2016). The relationship between testosterone and long-distance calling in wild male chimpanzees. *Behavioral Ecology and Sociobiology*, **70**(5), 659-672.

Fitch, W. T., Neubauer, J., & Herzel, H. (2002). Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour*, *63*(3), 407-418.

Flower, T. P., Gribble, M., & Ridley, A. R. (2014). Deception by flexible alarm mimicry in an African bird. *Science*, **344**(6183), 513-516.

Freeberg, T. M., Dunbar, R. I., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity, 367(1597).

Frey, R., Volodin, I. A., Volodina, E. V., Efremova, K. O., Menges, V., Portas, R., & von Dörnberg, K. (2020). Savannah roars: The vocal anatomy and the impressive rutting calls of male impala (*Aepyceros melampus*)–highlighting the acoustic correlates of a mobile larynx. *Journal of Anatomy*, **236**(3), 398-424.

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, **7**(11), 1325-1330.

Gamba, M., Torti, V., Estienne, V., Randrianarison, R. M., Valente, D., Rovara, P., & Giacoma, C. (2016). The indris have got rhythm! Timing and pitch variation of a primate song examined between sexes and age classes. *Frontiers in Neuroscience*, **10**, 249.

Garland, E. C., & McGregor, P. K. (2020). Cultural transmission, evolution, and revolution in vocal displays: insights from bird and whale song. *Frontiers in Psychology*, **11**, 2387.

Giacoma, C., Sorrentino, V., Rabarivola, C., & Gamba, M. (2010). Sex differences in the song of Indri indri. *International Journal of Primatology*, **31**(4), 539-551.

Gil, D., & Gahr, M. (2002). The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution*, **17**(3), 133-141.

Gould, S. J., & Vrba, E. S. (1982). Exaptation—a missing term in the science of form. *Paleobiology*, **8**(1), 4-15.

Grafe, T. U., & Wanger, T. C. (2007). Multimodal signaling in male and female foot‐flagging frogs *Staurois guttatus* (Ranidae): An alerting function of calling. *Ethology*, **113**(8), 772-781.

Guilford, T., & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour*, **42**(1), 1-14.

Gustison, M. L., le Roux, A., & Bergman, T. J. (2012). Derived vocalizations of geladas (*Theropithecus gelada*) and the evolution of vocal complexity in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**(1597), 1847-1859.

Gustison, M. L., & Bergman, T. J. (2016). Vocal complexity influences female responses to gelada male calls. *Scientific Reports*, **6**, 19680.

Gyger, M., Karakashian, S. J., Dufty Jr, A. M., & Marler, P. (1988). Alarm signals in birds: the role of testosterone. *Hormones and Behavior*, **22**(3), 305-314.

Hebets, E. A. (2004). Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behavioral Ecology*, **16**(1), 75-82.

Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, **57**(3), 197-214.

Hebets, E. A., Barron, A. B., Balakrishnan, C. N., Hauber, M. E., Mason, P. H., & Hoke, K. L. (2016). A systems approach to animal communication. *Proceedings of the Royal Society B: Biological Sciences*, **283**(1826), 20152889.

Herman, L. M. (2017). The multiple functions of male song within the humpback whale (M egaptera novaeangliae) mating system: review, evaluation, and synthesis. *Biological Reviews*, **92**(3), 1795-1818.

Hill, S. D., Brunton, D. H., Anderson, M. G., & Ji, W. (2018). Fighting talk: complex song elicits more aggressive responses in a vocally complex songbird. *Ibis*, **160**(2), 257-268.

Jarman, M. V. (1979). *Impala social behaviour: territory, hierarchy, mating, and the use of space*. Parey.

Johnstone, R. A. (1996). Multiple displays in animal communication:'backup signals' and 'multiple messages'. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **351**(1337), 329-338.

Kingdon, J. (1982). *East African mammals: an atlas of evolution in Africa, Volume 3, Part C: Bovids*. University of Chicago Press.

Kitchen, D. M., da Cunha, R. G. T., Holzmann, I., & de Oliveira, D. A. G. (2015). Function of loud calls in howler monkeys. In *Howler Monkeys* (pp. 369-399). Springer, New York, NY.

Krebs, J. R. (1982). Territorial defence in the great tit (*Parus major*): do residents always win?. *Behavioral Ecology and Sociobiology*, **11**(3), 185-194.

Kutner, M. H., Nachtsheim, C. J., & Neter, J. (2005). *Applied linear regression models (4th Edition)*. Irwin/McGraw-Hill, New York, NY.

Lenth, R., & Lenth, M. R. (2018). Package 'lsmeans'. *The American Statistician*, **34**(4), 216-221.

Leuthold, W. (1977). *African ungulates: a comparative review of their ethology and behavioral ecology* (Vol. 8). Springer Science & Business Media.

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., & Brooks, M. (2019). Package'glmmTMB': Generalized Linear Mixed Models using Template Model Builder. *The Comprehensive R Archive Network*.

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews*, **90**(2), 560-586.

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**(1483), 2315-2324.Manser, M. B. (2016). Call concatenation in non-primate mammals. *The Journal of the Acoustical Society of America*, **140**(4), 3240-3240.

Manser, M. B., Jansen, D. A., Graw, B., Hollén, L. I., Bousquet, C. A., Furrer, R. D., & le Roux, A. (2014). Vocal complexity in meerkats and other mongoose species. *Advances in the Study of Behavior*, **46**, 281-310). Academic Press.

Marler, P. (1972). Vocalizations of East African monkeys II: black and white colobus. *Behaviour*, **42**(3-4), 175-197.

Marler, P., & Mitani, J. C. (1989). A phonological analysis of male gibbon singing behavior. *Behaviour*, **109**(1-2), 20-45.

Marler, P. R., & Slabbekoorn, H. (2004). *Nature's music: the science of birdsong*. Elsevier.

Maynard-Smith, J. (1979). Game theory and the evolution of behaviour. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **205**(1161), 475-488.

McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters*, **1**(4), 381-385.

McCulloch, C. E., & Neuhaus, J. M. (2005). Generalized linear mixed models. *Encyclopedia of biostatistics*, **4**.

Meise, K., Franks, D. W., & Bro-Jørgensen, J. (2018). Multiple adaptive and non-adaptive processes determine responsiveness to heterospecific alarm calls in African savannah herbivores. *Proceedings of the Royal Society B: Biological Sciences*, **285**(1882), 20172676.

Miles, H. L. (1986). How can I tell a lie? Apes, language and the problem of deception. In Mitchell, R. V., & Thomson, R. S. (Eds). *Deception: Perspectives on human and nonhuman deceit*, 245-266. Suny Press, Albany.

Mitani, J. C. (1985). Sexual selection and adult male orangutan long calls. *Animal Behaviour*, **33**(1), 272-283.

Mokkonen, M., & Lindstedt, C. (2016). The evolutionary ecology of deception. *Biological Reviews*, **91**(4), 1020-1035.

Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist*, **111**(981), 855-869.

Munn, C. A. (1986). Birds that 'cry wolf'. *Nature*, **319**(6049), 143-145.

Murray, M. G. (1982). The rut of impala: aspects of seasonal mating under tropical conditions. *Zeitschrift für Tierpsychologie*, **59**(4), 319-337.

Murtaugh, P. A. (2014). In defense of P values. *Ecology*, **95**(3), 611-617.

Nelson, D. A. (2017). Geographical variation in song phrases differs with their function in white-crowned sparrow song. *Animal Behaviour*, **124**, 263-271.

Ogutu, J. O., Owen-Smith, N., Piepho, H. P., & Dublin, H. T. (2015). How rainfall variation influences reproductive patterns of African savanna ungulates in an equatorial region where photoperiod variation is absent. *PloS One*, **10**(8), e0133744.

Oliver, C. M., Skinner, J. D., & Van der Merwe, D. (2007). Territorial behaviour in southern impala rams (*Aepyceros melampus* Lichtenstein). *African Journal of Ecology*, **45**(2), 142-148.

Ord, T. J., & Stamps, J. A. (2008). Alert signals enhance animal communication in "noisy" environments. *Proceedings of the National Academy of Sciences*, **105**(48), 18830-18835.

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's monkeys use affixation to alter call meaning. *PloS One*, **4**(11), e7808.

Owen-Smith, N. (1977). On territoriality in ungulates and an evolutionary model. *The Quarterly Review of Biology*, **52**(1), 1-38.

Palmer, M. S., & Gross, A. (2018). Eavesdropping in an African large mammal community: antipredator responses vary according to signaller reliability. *Animal Behaviour*, **137**, 1-9.

Passilongo, D., Reby, D., Carranza, J., & Apollonio, M. (2013). Roaring high and low: composition and possible functions of the Iberian stag's vocal repertoire. *PloS One*, **8**(5), e63841.

Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist*, **166**(2), 231-245.

R Development Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Read, A. F., & Weary, D. M. (1992). The evolution of bird song: comparative analyses. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **338**(1284), 165-187.

Reby, D., & McComb, K. (2003). Vocal communication and reproduction in deer. *Advances in the Study of Behavior*, **33**, 231-264.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T., & Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society B: Biological Sciences*, **272**(1566), 941-947.

Reby, D., & Charlton, B. D. (2012). Attention grabbing in red deer sexual calls. *Animal Cognition*, **15**(2), 265-270.

Richards, D. G. (1981). Alerting and message components in songs of rufous-sided towhees. *Behaviour*, **76**(3-4), 223-249.

Sainburg, T., Theilman, B., Thielk, M., & Gentner, T. Q. (2019). Parallels in the sequential organization of birdsong and human speech. *Nature Communications*, **10**(1), 1-11.

Schenkel, R. (1966). On sociology and behaviour in impala. *African Wildlife Journal*, **4**, 99-114.

Schlenker, P., Chemla, E., & Zuberbühler, K. (2016). What do monkey calls mean?. *Trends in Cognitive Sciences*, **20**(12), 894-904.

Schlenker, P., Chemla, E., Cäsar, C., Ryder, R., & Zuberbühler, K. (2017). Titi semantics: Context and meaning in Titi monkey call sequences. *Natural Language & Linguistic Theory*, **35**(1), 271-298.

Searcy, W. A., & Andersson, M. (1986). Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, **17**(1), 507-533.

Searcy, W. A., & Nowicki, S. (2019). Birdsong learning, avian cognition and the evolution of language. *Animal Behaviour*, **51**, 217-227.

Semple, S., & McComb, K. (1996). Behavioural deception. *Trends in Ecology & Evolution*, **11**(10), 434-437.

Seyfarth, R. M., & Cheney, D. L. (2017). Precursors to language: Social cognition and pragmatic inference in primates. *Psychonomic Bulletin & Review*, **24**(1), 79-84.

Sherman, P. W. (1985). Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation?. *Behavioral Ecology and Sociobiology*, **17**(4), 313-323.

Slocombe, K. E., & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, **104**(43), 17228-17233.

Soma, M., & Garamszegi, L. Z. (2011). Rethinking birdsong evolution: meta-analysis of the relationship between song complexity and reproductive success. *Behavioral Ecology*, **22**(2), 363-371.

Townsend, S. W., & Manser, M. B. (2011). The function of nonlinear phenomena in meerkat alarm calls. *Biology Letters*, **7**(1), 47-49.

Vannoni, E., & McElligott, A. G. (2008). Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. *PloS one*, **3**(9).

Volodina, E. V., Volodin, I. A., Chelysheva, E. V., & Frey, R. (2018). Hiss and snort call types of wild-living giraffes Giraffa camelopardalis: acoustic structure and context. *BMC Research Notes*, **11**(1), 12.

Walther, F. R. (1984). *Communication and expression in hoofed mammals*. Indiana University Press.

Wheeler, B. C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B: Biological Sciences*, **276**(1669), 3013-3018.

Wiley, R. H. (2013). Signal detection, noise, and the evolution of communication. In Bruhm, H. (Ed) *Animal communication and noise*. 7-30. Springer, Berlin, Heidelberg.

Yau, K. K., Wang, K., & Lee, A. H. (2003). Zero-inflated negative binomial mixed regression modeling of over-dispersed count data with extra zeros. *Biometrical Journal: Journal of Mathematical Methods in Biosciences*, **45**(4), 437-452.

Zuberbühler, K., & Lemasson, A. (2014). Primate communication: Meaning from strings of calls. In *Language and recursion*, 115-125. Springer, New York, NY.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Zero-truncated and zero-inflated models for count data. In *Mixed effects models and extensions in ecology with R* (pp. 261-293). Springer, New York, NY.

4.9 APPENDIX I

Playback stimuli construction

Playback stimuli of male impala roaring displays (snorts + grunts) were obtained by manipulating high-quality recordings from 8 different individuals. The recordings were edited as to reflect variation in call duration, while respecting the structure and arrangement of the single vocalizations. Acoustic characteristics of the calls were measured in Praat 6.0.4 (Boersma & Weenink 2017), while sound editing was conducted in Audacity 2.1.0 (Audacity Development Team 2017).

All available recordings of roaring displays from the study area (n = 36; including low-quality exemplars) began with a snort or a sequence of snorts (range = 1-13 snorts; cf. Schenkel 1966; Jarman 1979; Frey et al. 2020). I therefore edited the recordings in order to include both a small number (1) and a large number (10) of snorts, mimicking natural variation. Silent intervals between snorts were standardized to an average duration (0.387 seconds). Similarly, the silent interval between the snorts and the following grunts was standardized to the average value (0.302 seconds). Single snorts were not altered during the editing process.

Snorts were followed by a grunting call in all recordings of roaring displays (although additional snorts sometimes also followed grunts; Frey et al. 2020; G. D'Ammando pers. obs.). Grunts are multi-syllable vocalizations (range = 2-20 syllables) emitted through a mobile larynx (Frey et al. 2020; G. D'Ammando, pers. obs.). Larynx retraction generates vocal tract elongation, reflected by a gradual decrease in formant frequencies (similarly to other bovids and cervids with retractable larynxes; Reby et al. 2005; McElligott et al. 2006; Vannoni & McElligott 2008; Frey et al. 2009, 2011). Using the "To Formants (Burg)" command in Praat (Maximum Formant = 5000 Hz; number of formants = 6; window length = 0.025 s; Frey et al. 2020), I was thus able to distinguish different types of syllables according to the shape of formants and the position in the grunt. All grunts presented a syllable with descending formants at the beginning (introductory phase), a series of syllables with stable formants in the middle (middle phase), and a syllable with ascending formants at the end (final phase; cf. Frey et al. 2020).

I edited recordings in order to obtain grunts containing a varying number of syllables, while respecting the observed arrangement into an introductory, middle, and final phase. Three exemplars included only 2 syllables (introductory and final phases), and were left unmodified for playbacks. The other five exemplars were standardized to either a 4-syllable grunt (introductory and final phases plus two middle syllables); a 16-syllable call (introductory and final phases plus fourteen middle syllables). This corresponded to small and large numbers of syllables within the observed range of variation. The roaring display stimuli used during playbacks therefore included the following combinations:

(i) 1 snort + 2 syllable grunt;
(ii) 1 snort + 4 syllable grunt;
(iii) 1 snort + 16 syllable grunt;
Grunt-dominated roaring displays

(iv) 10 snorts + 2 syllable grunt;
(v) 10 snorts + 4 syllable grunt;
(vi) 10 snorts + 16 syllables grunt.
Snort-dominated roaring displays

All stimuli were kept at <15 s in maximum duration in order to avoid unnecessary disturbance to the animals.

4.10 APPENDIX II

Individual identification of territorial male impala

Playback trials were conducted on unmarked individual male impala. Under ideal conditions, individually-identified males should have been repeatedly located on different days and presented with different playback stimuli. However, impala in the Mara proved impossible to be tracked on a daily basis, most probably owing to short territorial tenure (13 days to 3 months; Jarman 1979; Kingdon 2015), and to the dense thickets where individuals could remain hidden for long periods. I therefore opted to minimize the possibility of exposing the same individual males to playback trials by: (i) avoiding presentation of stimuli to males with the same body characteristics; and (ii) ensuring a high level of spatial and temporal segregation between playback trials. Distinctive horn shape and horn ridging, and the presence and location of ear notches/tears and albinisms, and of prominent scars, were all noticed and reported on custom-made identity cards. Individuals with matching characteristics were not presented with more than one playback. On the same day of experiments, the same route was never followed twice in order to avoid re-sampling the same individuals; playback sites were spaced at a minimum distance of 800 m (beyond the observed active sound space of impala calls, as per direct observations in conditions of low wind; G. D'Ammando, pers. obs.). The GPS location of experimental trials was also recorded, so that, on different days, playback trials were not conducted within 80 m of previous ones. This distance was larger than the estimated diameter of the largest estimated male impala territory (800 m^2) in the Serengeti-Mara ecosystem (Jarman 1979; Estes 1991). These combined precautionary measures should have thus likely minimized the possibility for pseudo-replication.

In order to limit my playback experiments to territorial males, I searched for males with fully-grown lyrate horns (≥ 3.5 years old; Spinage 1971); and which were either solitary (with no other adult males were visible within ~100 m) or tending to a harem of females (males in bachelor herds were excluded). Territorial status was inferred by observing male impala for a minimum of 10 minutes prior to playback presentation. This allowed me to confirm territorial status by observing typical traits connected with territoriality, namely: (i) "proud" posture in elevated terrain; (ii) linked urination-defecation displays; and (iii) dark skin patches around the eyes (Jarman 1979). Only individuals which exhibited at least two of these traits were deemed as territorial and selected for playback trials.

References

Audacity Development Team (2017). Audacity(R): Free Audio Editor and Recorder [Computer application]. Version 2.1.0. URL: https://audacityteam.org/ [1].

Boersma, Paul & Weenink, David (2017). Praat: doing phonetics by computer [Computer program]. Version 6.0.4. URL: http://www.praat.org/.

Bro-Jørgensen, J., & Durant, S. M. (2003). Mating strategies of topi bulls: getting in the centre of attention. *Animal Behaviour*, **65**(3), 585-594.

Carrasco, M. F., & Blumstein, D. T. (2012). Mule deer (*Odocoileus hemionus*) respond to yellow-bellied marmot (*Marmota flaviventris*) alarm calls. *Ethology*, *118*(3), 243-250.

Estes, R. D. (1991). *The Behaviour Guide to African Mammals*. University of California Press, Berkeley (USA).

Frey, R., Gebler, A., Olson, K. A., Odonkhuu, D., Fritsch, G., Batsaikhan, N., & Stuermer, I. W. (2008). Mobile larynx in Mongolian gazelle: retraction of the larynx during rutting barks in male Mongolian gazelle (*Procapra gutturosa* Pallas, 1777). *Journal of Morphology*, **269**(10), 1223-1237.

Frey, R., Volodin, I., Volodina, E., Soldatova, N. V., & Juldaschev, E. T. (2011). Descended and mobile larynx, vocal tract elongation and rutting roars in male goitred gazelles (*Gazella subgutturosa* Güldenstaedt, 1780). *Journal of Anatomy*, **218**(5), 566-585.

Frey, R., Volodin, I. A., Volodina, E. V., Efremova, K. O., Menges, V., Portas, R., & von Dörnberg, K. (2020). Savannah roars: The vocal anatomy and the impressive rutting calls of male impala (*Aepyceros melampus*)–highlighting the acoustic correlates of a mobile larynx. *Journal of Anatomy*, **236**(3), 398-424.

Jarman, M. V. (1979). *Impala social behaviour: territory, hierarchy, mating, and the use of space*. Parey.

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.

McElligott, A. G., Birrer, M., & Vannoni, E. (2006). Retraction of the mobile descended larynx during groaning enables fallow bucks (*Dama dama*) to lower their formant frequencies. *Journal of Zoology*, **270**(2), 340-345.

Meise, K., Franks, D. W., & Bro-Jørgensen, J. (2018). Multiple adaptive and non-adaptive processes determine responsiveness to heterospecific alarm calls in African savannah herbivores. *Proceedings of the Royal Society B: Biological Sciences*, **285**(1882), 20172676.

Murray, M. G. (1981). Structure of association in impala, *Aepyceros melampus*. *Behavioral Ecology and Sociobiology*, **9**(1), 23-33.

Palmer, M. S., & Gross, A. (2018). Eavesdropping in an African large mammal community: antipredator responses vary according to signaller reliability. *Animal Behaviour*, **137**, 1-9.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T., & Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society B: Biological Sciences*, **272**(1566), 941-947.

Spinage, C. A. (1971). Geratodontology and horn growth of the impala (*Aepyceros melampus*). *Journal of Zoology*, **164**(2), 209-225.

Vannoni, E., & McElligott, A. G. (2008). Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. *PloS One*, **3**(9), e3113.

CHAPTER 5: HUMAN SHIELDS ASSOCIATED WITH LOWER VIGILANCE, BUT STRONGER ALARM CALL RESPONSES, IN TWO AFRICAN ANTELOPES

ABSTRACT

Anthropogenic activities can lead to substantial alterations in antipredator behaviour, with relevant implications for the conservation and management of wildlife populations. The antipredator responses of wild ungulates might be reduced by so-called ‘shielding effects’ in the proximity of human settlements, caused by the extirpation of large carnivores. Here I investigated whether human shieldsat the borders of the Maasai Mara National Reserve (Kenya) affected two antipredator behaviours, vigilance and responsiveness to alarm calls, in two savannah antelopes, the topi (*Damaliscus lunatus*) and the Thomson’s gazelle (*Eudorcas thomsonii*). I compared vigilance levels and reactions to playbacks of both conspecific and heterospecific alarm calls between “disturbed areas” along the boundaries of the reserve, where conflicts with pastoralists had depressed the abundance of predators; and “undisturbed areas” at the core of the reserve away from human settlements. I found that both species were less vigilant in disturbed than in undisturbed areas, indicating a reduction in the overall exposure to predation risk. However, contrary to my expectations, the two antelopes responded more strongly to conspecific alarm calls in disturbed areas. I suggest that alarm calls in disturbed areas might denote unpredictable anthropogenic threats, and therefore require more careful assessment. No detectable differences in reactions to heterospecific alarm calls between disturbed and undisturbed areas may reflect less finely tuned responses to such less important calls.

5.1 INTRODUCTION

Wildlife is increasingly coming into contact with humans due to global population growth and encroachment into natural habitats (Ceballos & Ehrlich 2002; Nyhus 2016; Margulies & Karanth 2018; Treves & Santiago-Avila 2020). Some anthropogenic activities represent a major source of disturbance to terrestrial vertebrates, and can lead to profound behavioural alterations (Cooke et al. 2014; Stabach et al. 2016; Greenberg & Holekamp 2017; Paton et al. 2017; Benitez-Lopez 2018; Gaynor et al. 2018; Marion et al. 2020). For example, hunting and human-wildlife conflicts can instil strong fear in large mammals, causing substantial intensifications in risk-sensitive behaviours (e.g. vigilance rates: Ciuti et al. 2012a, 2012b; Crosmary et al. 2012; Schuttler et al. 2017). By contrast, more benign forms of disturbance, such as urbanization and nature-based tourism, often coincide with a relaxation of overall alertness to danger (Thompson & Henderson 1998; Lowry, Lil & Wong 2013; Hansen & Aanes 2015; Uchida et al. 2019; Wevers et al. 2020; Berger et al. 2020). This is likely a consequence of "shielding effects" against natural predators implemented via the eradication or deterrence of large mammalian carnivores from human-dominated landscapes (Berger 2007; Atickem, Loe & Stenseth 2014; Sarmento, Biel & Berger 2016; Berger et al. 2020). On these premises, conservationists have voiced concerns over the potential for human shields to interfere with the ability of prey species to correctly discriminate and assess cues and signals of predation risk (Coleman et al. 2008; Carrasco & Blumstein 2012; Geffroy et al. 2015; Carthey & Blumstein 2018). In this study, I addressed whether shielding effects in a protected area could have dampened the responsiveness to alarm calls in two species of African antelopes.

Several studies have demonstrated that wild ungulates perceive settlements and other anthropogenic infrastructures as safe refuges from natural predators, since large mammalian carnivores, following a long history of persecution, tend to avoid human presence (e.g. Ordiz et al. 2011; Wilmers et al. 2013; Oriol-Cotterill et al. 2015; Gehr et al. 2017). Accordingly, ungulate populations in agricultural or urban contexts are significantly less vigilant than those inhabiting more pristine wilderness (Shannon et al. 2014; Saltz et al. 2019). Some evidence also exists that shielding effects can diminish ungulate sensitivity to interactions with predators: mountain goats (*Oreamnos americanus*) are less prone to flee from grizzly bears (*Ursus arctos*) at tourist sites from which the latter are actively deterred (Sarmento & Berger 2017). However, the impact of human shields on antipredator signals remains poorly understood.

Ungulates emit alarm calls primarily as notifications of detection to ambush predators (relying on stealth), signalling the loss of the surprise element and the unprofitability of launching an attack (Caro 1994; Bro-Jørgensen & Pangle 2010). In social species, group members also become immediately alert after hearing an alarm call, gleaning information about imminent threats (Caro et al. 1995; Bro-Jørgensen & Pangle 2010). The same occurs in mixed-species herds, where individuals often rely on the signalling behaviour of heterospecifics in order to locate approaching predators (Palmer & Gross 2018; Meise, Franks & Bro-Jørgensen 2018). The strength of the responses to alarm calls would be expected to reflect the severity of the threat associated with the signal (Meise et al. 2018). Here I propose that if human shields reduce the likelihood of encountering natural predators, alarm calls would become associated with less severe threats, and therefore elicit attenuated reactions.

The Maasai Mara National Reserve (Kenya; the Mara from now onwards) offers an ideal setting to test the potential for human shields to affect ungulate alarm call responses. Along its north-eastern boundaries, the Mara is characterized by the large-scale livestock herding practices of local Maasai communities, connected with a sprawling growth of urban centres (Butt & Turner 2012; Butt 2014; Green et al. 2019; Veldhuis et al. 2019). Maasai pastoralists do not usually hunt wild ungulates (Ceppi & Nielsen 2014; Kiffner et al. 2015), but regularly persecute large carnivores (Mogensen, Ogutu & Dabelsteen 2011; Mukeka et al. 2019; Broekhuis et al. 2020), leading to markedly reduced density of of some predator species in areas of the reserve next to unprotected village land (Ogutu, Bhola & Rheid 2005; Green et al. 2018). At the same time, the core regions of the Mara are relatively inaccessible to herders and unaffected by conflicts with predators (Farr et al. 2019). I therefore compared the vigilance behaviour and the reactions to playbacks of alarm calls of two abundant antelopes, the topi (*Damaliscus lunatus*) and the Thomson's gazelle (*Eudorcas thomsonii*), between "disturbed areas" at the periphery of the Mara, presumed to be relatively shielded against natural predators, and "undisturbed areas" away from settlements. I expected that, if topi and Thomson's gazelles benefit from human shields, baseline vigilance levels would be lower in disturbed areas near humans, than in the undisturbed core regions of the reserve. I also predicted weaker responses to alarm calls in disturbed areas, assuming that signals of predation risk were more likely to be elicited by less dangerous stimuli. Furthermore, given the overlapping information content in the alarm calls of the two study species (i.e. they largely denote the same predators; Meise et al. 2018), I predicted that shielding effects should have a similar effect on the responsiveness to both conspecific and heterospecific alarm calls.

5.2 METHODS

Study area

The Mara is an unfenced protected area covering expanses of short and tall grassland, interspersed with patches of thickets and riparian forests. The reserve is traversed by the Talek River, and the Mara River forms its Western border. The area is characterized by bimodal rainfall patterns, peaking in November-December and March-May. The present study was conducted between November 2017 and May 2018, thus coinciding with the period of high rainfall. Pastoralist settlements are concentrated in the unprotected Talek Enclave, which has seen a burgeoning increase in human and livestock populations over the last two decades (Pangle & Holekamp 2010; Green et al. 2019).

Topi and gazelles are common year-round in all areas of the Mara (Green et al. 2019). These antelopes are usually found in open plains, and frequently aggregate in mixed-species herds (Estes 1991). Both species regularly emit alarm calls at the sight of ambush predators, which in the Mara include lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), and leopard (*Panthera pardus*; Estes 1991; Meise et al. 2018).

Selection of disturbed and undisturbed areas

Two open plains along the boundaries of the Mara with the Talek Enclave were selected as "disturbed areas". These areas were exposed to livestock grazing, according to maps of livestock distribution made available by the Mara Predator Conservation Programme (www.marapredatorconservation.org), published evidence (Butt 2010, 2014), and personal observations. All playback trials and vigilance observations were conducted within 1.5 km of the heavily settled Talek town. In order to represent undisturbed areas, I chose three open plains, all > 15 km away from the border with the Talek Enclave, well beyond the maximum penetration range of pastoralists and their herds (~ 6 km; Pangle & Holekamp 2010, www.marapredatorconservation.org). This distance also ensured limited movements between disturbed and undisturbed areas for both study species, based on estimated home range diameter (~ 3 km for resident populations of Thomson's gazelles; Walther 1972; 7 km for the topi; Bro-Jørgensen 2003). Individuals in the two areas were thus assumed to have experienced markedly different levels of human activity over their lifetime.

Baseline vigilance observations

I recorded vigilance behaviour during grazing bouts (duration = 5 minutes) on a digital video camera (Sony HDR-PJ810E) for ten different topi and gazelles (5 males, 5 females) in disturbed and undisturbed areas, respectively. Observations were limited to individuals in small herds (≤ 4 individuals), and at sites with grass ≤ 30 cm, in order to exclude confounding effects on vigilance of group size (Hunter & Skinner 1998; Creel, Schuette & Christianson 2014; no significant associations were found between vigilance and minimal group sizes, topi: z = 0.258, n = 10, p =0.796; gazelle: z = 0.326, n = 10, p = 0.745) and grass height, with taller grass providing cover for ambush predators (Funston, Mills & Biggs 2001; Meise et al. 2018). The rate of head-lifts (at shoulder level and above) during grazing bouts was considered as an indicator of baseline vigilance levels.

Playback stimuli

Exemplars of alarm calls from six different individual gazelles and topi (three from each sex) were recorded during the course of a previous study (Meise et al. 2018; **Fig. 1**). Each of these two species has a highly stereotypic alarm call, without obvious differences in acoustic structure between calls elicited by different predator species (Estes 1991; Meise et al. 2018). Recorded vocalizations of the ring-necked dove (*Streptopelia capicola*), comparable in volume to the alarm calls, were used as control sounds (Meise et al. 2018; **Fig. 1**). All playback stimuli were standardized to natural amplitudes measured in the field at a 35 m distance, using a handheld recorder (UNI-T, model UT352).

Playback experiments

I conducted a total of 144 playback trials. Each stimulus (topi, gazelle, and dove) was presented to 11-13 different adult individuals per species in each area (disturbed and undisturbed), balancing trials between males and females (stimulus per sex per area: range = 5-6). In order to minimize the risk of pseudo-replication, individual exemplars, which were presented in a randomized order, were not played more than three times to the same species in the same area, and I noted down visible morphological traits (shape of the horns, forehead markings, presence of albinisms, visible scars; Walther, Mungall & Grau 1983; Bro-Jørgensen & Durant 2003) to ensure that each playback trial was conducted on individuals not previously targeted. I also travelled >250 m between playback trials on the same day (beyond the active space of alarm calls; Meise et al. 2018), and visited the same plains at a minimum of five-day intervals. For male antelopes, I focused on territorial individuals (recognizable by distinctive behaviours; Estes 1991; Bro-Jørgensen 2003), and played back stimuli on different days at distances larger than the estimated territory diameters (Walther 1972; Bro-Jørgensen 2003). Considering also the very large population of the two study species in the Mara (Bhola et al. 2012), the risk of pseudo-replication affecting the results in this study is minimal.

Adult topi and gazelles were located while driving along the existing road network of the Mara. I selected the closest grazing animal in a relaxed and stationary herd as the focal individual, and played back the stimulus after a 20s period of uninterrupted grazing (Meise et al. 2018). Stimuli were broadcasted using a digital audio recorder (Tascam H2-P2) connected to a loudspeaker (Mipro MA707) positioned at ground level and hidden by the car silhouette (ungulates in the Mara are habituated to vehicles; Bro-Jørgensen & Pangle 2010). All trials were recorded on a digital video camera (Sony HDR-PJ810E). To ensure stimulus detection, playbacks were conducted at distances of 45-80 m (measured with a laser rangefinder, Bushnell Scout DX 1000 ARC), and at a wind speed of ≤ 3 m/s (measured with an anemometer, Proster Digital Lcd Meise et al. 2018). I also estimated grass height, distance from vegetation cover, and group size at each playback site (Appendix).

Behavioural analyses

Videos from playback trials were processed in BORIS (Behavioural Observation Research Interface Software; Friard & Gamba 2016) using frame-by-frame analysis (temporal window length = 0.04 s). A response was scored as occurring if focal individuals lifted their head at shoulder level within 10 seconds from the onset of the stimulus. Response intensity was measured as: (i) response latency (time to head-lifting); and (ii) response duration (interval between head-lifting, and first head-lowering to resume grazing; Meise et al. 2018).

Responses to controls

I found that topi and gazelles lifted their heads significantly more often after playback of alarm calls, than after playback of the control dove sound (topi: $\chi^2 = 32.237$, $p < 0.001$; gazelle: $\chi^2 = 27.036$, $p < 0.001$). Additionally, individuals of both study species were not more likely to lift their heads after playback of the control sound than during randomly-selected 10 second intervals from grazing bouts (topi in disturbed areas: $\chi^2 = 0.002$, $p = 0.961$; topi in undisturbed areas: $\chi^2 = 0.000$, $p = 1.000$; gazelle in disturbed areas: $\chi^2 = 0.552$, $p = 0.458$; gazelle in undisturbed areas: $\chi^2 = 0.000$, $p = 1.000$). These patterns support that the playback itself does not elicit responses and that heightened responsiveness is due to the information contained in the alarm calls.

Statistical analyses

All statistical analyses were conducted in R v. 3.5.2 (R Development Core Team, 2019). I compared response latency to alarm calls (re-scaled from seconds to milliseconds) between disturbed and undisturbed areas using the log-rank statistic of time-to-event Kaplan-Meyer survival analysis, in the packages survival and survminer (Therneau & Lumley 2014; Kassambara et al. 2017). In case of no response, data were considered as right-censored, and entered in the model with a value of 10 000 milliseconds (the maximum cut-off point I allowed for a response to occur). Response duration to conspecific and heterospecific alarm calls was compared between areas using unpaired Wilcoxon rank-signed sum tests (statistical significance was set at $p \leq 0.05$). Wilcoxon rank-signed sum tests were also applied to compare differences in the number of head-lifts during grazing bouts according to the level of human disturbance.

The relatively small sample size (23-25 playback trials per each combination of stimulus - receiver) prevented the use of multivariate analyses to account for the simultaneous effects of multiple predictors on the intensity of the observed responses. In order to determine whether the impact of human disturbance could be confused by other factors, I therefore tested for differences in socio-ecological variables at playback sites between disturbed and undisturbed areas (distance to focal individual, group size, grass height, distance to vegetation cover, and wind speed), using Wilcoxon rank-signed sum tests. I then explored the potential correlations between these variables and the two measures of response strength (latency and duration) using Kendall's rank correlation tests.

5.3 RESULTS

Topi and gazelles living closer to humans lifted their head less often during grazing bouts than those in relatively undisturbed areas (topi in disturbed areas mean ± S.E. = 1.9 ± 0.458 head-lifts per bout; topi in undisturbed areas = 5.6 ± 0.6, $W = 7$, $p = 0.001$; gazelle in disturbed areas: 7.8 ± 0.8; gazelle in undisturbed areas: 15 ± 1.398; $W = 3.5$, $p = 0.0005$), in accordance with my predictions.

However, contrary to my expectations, topi and gazelles in disturbed areas exhibited stronger rather than weaker responses to conspecific alarm calls. Individuals of the two study species in the vicinity of humans were quicker to react to playbacks, although the difference was not significant for gazelles (topi: $\chi^2 = 12.100$,

$p < 0.001$; **Fig. 1A**; gazelle: $\chi^2 = 3.300$, $p = 0.071$; **Fig. 1B**). Responses to conspecific alarm calls also lasted for longer in disturbed areas for both topi (disturbed areas, mean ± S.E. = 39.941 ± 9.605 s; undisturbed areas = 13.215 ± 2.405 s; W = 111, $p = 0.023$; **Fig. 2A**) and gazelles (disturbed areas = 30.501 ± 6.49 s; udisturbed areas = 15.382 ± 4.737 s; W = 114, $p = 0.013$; **Fig. 2B**). On the other hand, human presence had no demonstrable effect on the reactions to heterospecific alarm calls, with no detectable differences found between disturbed and undisturbed areas in either response latency (topi to gazelle: $\chi^2 = 0.400$, $p = 0.530$, **Fig. 1C**; gazelle to topi: $\chi^2 = 0.000$, $p = 0.860$, **Fig. 1D**), or duration (topi to gazelle: W = 14, $p = 0.145$, **Fig. 2A**; gazelle to topi: W = 77, $p = 0.293$; **Fig. 2B**).

The majority of socio-ecological variables did not differ between disturbed and undisturbed areas, and showed no significant correlations with response latency and duration (Appendix): this suggests that my attempts at limiting variation in environmental conditions among playback sites were successful. An exception was made by grass height, significantly shorter in proximity to human settlements, likely due to livestock grazing pressures (Appendix). Ungulates are generally more reactive to antipredator signals in tall grass (providing ambush cover to predators): the stronger responses to conspecific alarm calls in disturbed areas therefore occurred in spite of the shorter grass, and most likely reflected genuine effects of human disturbance rather than differences in grass height (Appendix).

5.4 DISCUSSION

I found that human disturbance significantly influenced the vigilance behaviour and the responsiveness to alarm calls of topi and gazelles, though in opposite ways. Individuals of the two study species living in disturbed areas were less vigilant than those in undisturbed areas, but at the same time devoted heightened attention to playbacks of conspecific alarm calls. This was contrary to my expectation that a human shield against predation, provided by pastoralism and urbanization, would attenuate both antipredator behaviours. Moreover, exposure to humans did not modify the strength of the responses to heterospecific alarm calls.

The lower rate of head-lifts during grazing bouts suggests that topi and gazelles perceived areas around humans as safer from predation risk than those further away. As head-lifting in ungulates is generally aimed at preventing undetected approaches (Periquet et al. 2012; Owen-Smith 2019), these patterns likely reflected a decrease in the probability of encountering ambush predators (Berger, Swenson & Persson 2001; Shannon et al. 2014). In support of this claim, long-term monitoring has revealed a severe local decline in the population densities of all large carnivores relying on stealth to catch prey, most notably lion (*Panthera leo*) and cheetah (*Acinonyx jubatus*), in what I considered as "disturbed areas" (Broekhuis, Madsen & Klaassen 2019; Farr et al. 2019). The only exception is the spotted hyena (*Crocuta crocuta*); however, even if not affected numerically, this species still avoids pastoralists (Pangle & Holekamp 2010) and may in any case be less likely to affect vigilance levels as it adopts a coursing hunting strategy, not relying on ambush or stalking (FitzGibbon 1989; Droge et al. 2019). The results therefore corroborate the existence of human shields, at least against ambush predators, along the borders of the Mara.

In contrast to its effects on vigilance, proximity to humans appeared to increase the strength of topi and gazelle responses to conspecific alarm calls. Here I propose that anthropogenic threats, may introduce a higher degree of unpredictability to the information content of alarm calls, which may therefore require more intense scrutiny (Caro 2005; Bradbury & Vehrencamp 2011; Favreau-Peigne et al. 2016). Alarm calls of African antelopes are invariably elicited by both large carnivores and humans on foot (Caro 1994; Bro-Jørgensen & Pangle 2010; Meise et al. 2018). However, humans behave more unpredictably than natural predators, engaging in a wider variety of disturbances: some are relatively low cost to wild ungulates (e.g. harassment, nuisances), but others, even if infrequent, can be associated with extremely high mortality (notably shooting by firearms or bow-and-arrow; Proffitt et al. 2009; Zbyryt et al. 2018). This variability is likely to shape responses to alarm signals. Although hunting and wild meat consumption are rare among the Maasai (Kiffner et al. 2015), herders in the Mara also occasionally harass large herbivores due to perceived competition over forage resources (Okello 2005; Western et al. 2019). Additionally, livestock is often accompanied by unrestrained guarding dogs which are known to chase, injure, and sometimes kill wild ungulates (Pelletier 2006; Ekernas et al. 2017; Young et al. 2011; G. D'Ammando pers. obs.). Alarm calls in areas heavily used by pastoralists might have thus become associated with a less sustained but more diversified array of threatening situations (i.e. harassing humans, domestic dogs, sporadic predators) than those experienced at undisturbed sites (i.e. only natural predators). This could explain the observed combination of lower vigilance levels (threats are less common) and higher alertness to alarm calls (threats are more unpredictable) in disturbed areas. Following this interpretation, topi and gazelles co-existing with humans would have reacted more quickly and for longer to playbacks of alarm calls, in order to promptly assess the context of the signal, and to correctly evaluate the exact type of risk. Irrespectively of the reduced frequency of danger caused by shielding effects, the presentation of an alarm call would have therefore required a greater level of attention.

The human impact on alarm call responses was more marginal for gazelles than for topi (when considering response latencies). This might be explained by the fact that some gazelles range over long distances, encompassing both disturbed and undisturbed areas (Durant et al. 1988; Fryxell & Berdhal 2018). Nomadic/migratory individuals would have thus failed to develop responses specific to localized anthropogenic conditions.

As to why reactions to playbacks of heterospecific alarm calls were not affected by human disturbance, I can only advance speculative explanations. One possibility is that alarm calls of other species are heard less frequently than those of conspecifics, thereby limiting the opportunities for topi and gazelles to learn about potential associations with anthropogenic threats, and ultimately precluding the development of flexible adjustments in antipredator responses (Mery & Burns 2010; Magrath et al. 2015). Alternatively, ungulates could lack the cognitive ability to decipher subtle modifications in the communication system of another species (Heyes 1998; Seyfarth & Cheney 2010). As an example, vervet monkey (*Chlorocebus aethiops*) cease to react fearfully to their own alarm calls when repeatedly associated with non-threatening stimuli, but fail to do the same in response to the calls of familiar birds and antelopes (Cheney & Seyfarth 1992). Future studies are needed to confirm whether this is a general pattern.

5.5 CONCLUSION

This study provides evidence that even where human shields against predators reduce vigilance levels, they do not necessarily also reduce alarm call responsiveness, and may even increase it. An explanation for the increased attention paid to alarm calls BY ANTELOPES in human-dominated landscapes may be an association between these signals and more unpredictable anthropogenic threats. The extent to which human disturbance contribute to modify wildlife behaviour is a matter of on-going debates: my findings highlight that the impact of human presence on antipredator behaviours may be more complex than often assumed, and sometimes manifest itself in unexpected ways.

5.6 FIGURES

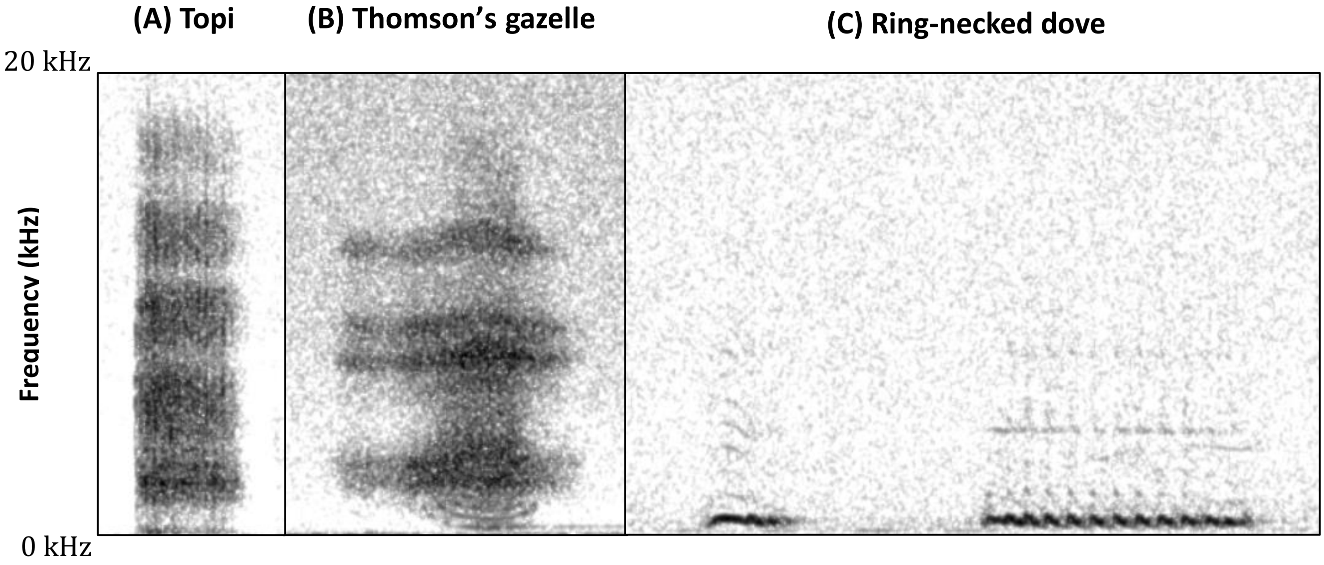


Figure 1: Spectrograms of stimulus exemplars used for playback experiments: (A) topi alarm call; (B) Thomson's gazelle alarm call; (C) ring-necked dove call (control sound). Spectrograms were generated in Praat version 6.1 (window length = 0.01 s; dynamic range = 50 dB).

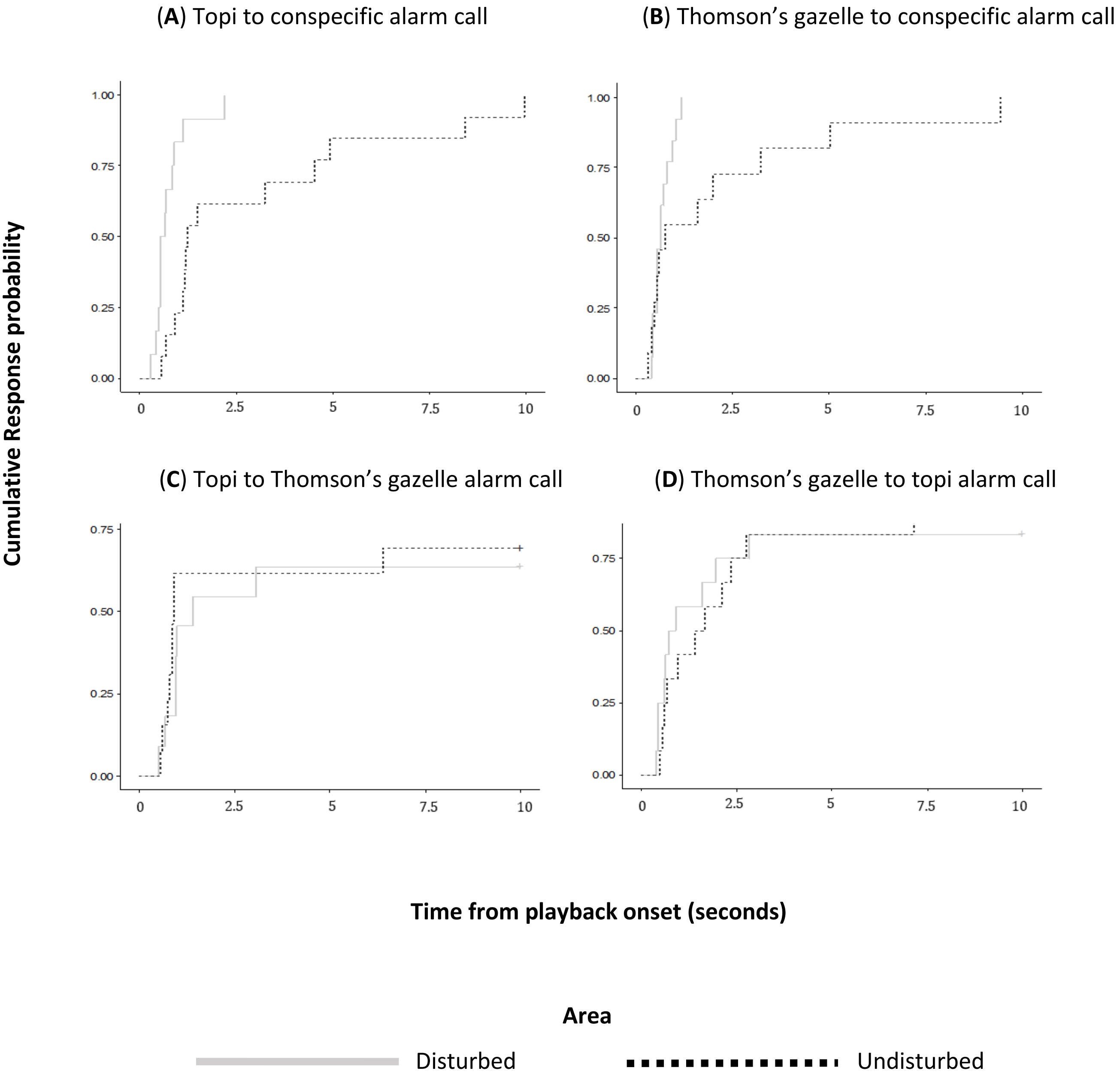


Figure 2: Cumulative incidence curves Kaplan-Meyer survival analysis comparing response latencies of topi and gazelles to playbacks of conspecific (A, B) and heterospecific alarm calls (C, D) between disturbed and undisturbed areas. Data are right-censored at 10 seconds.

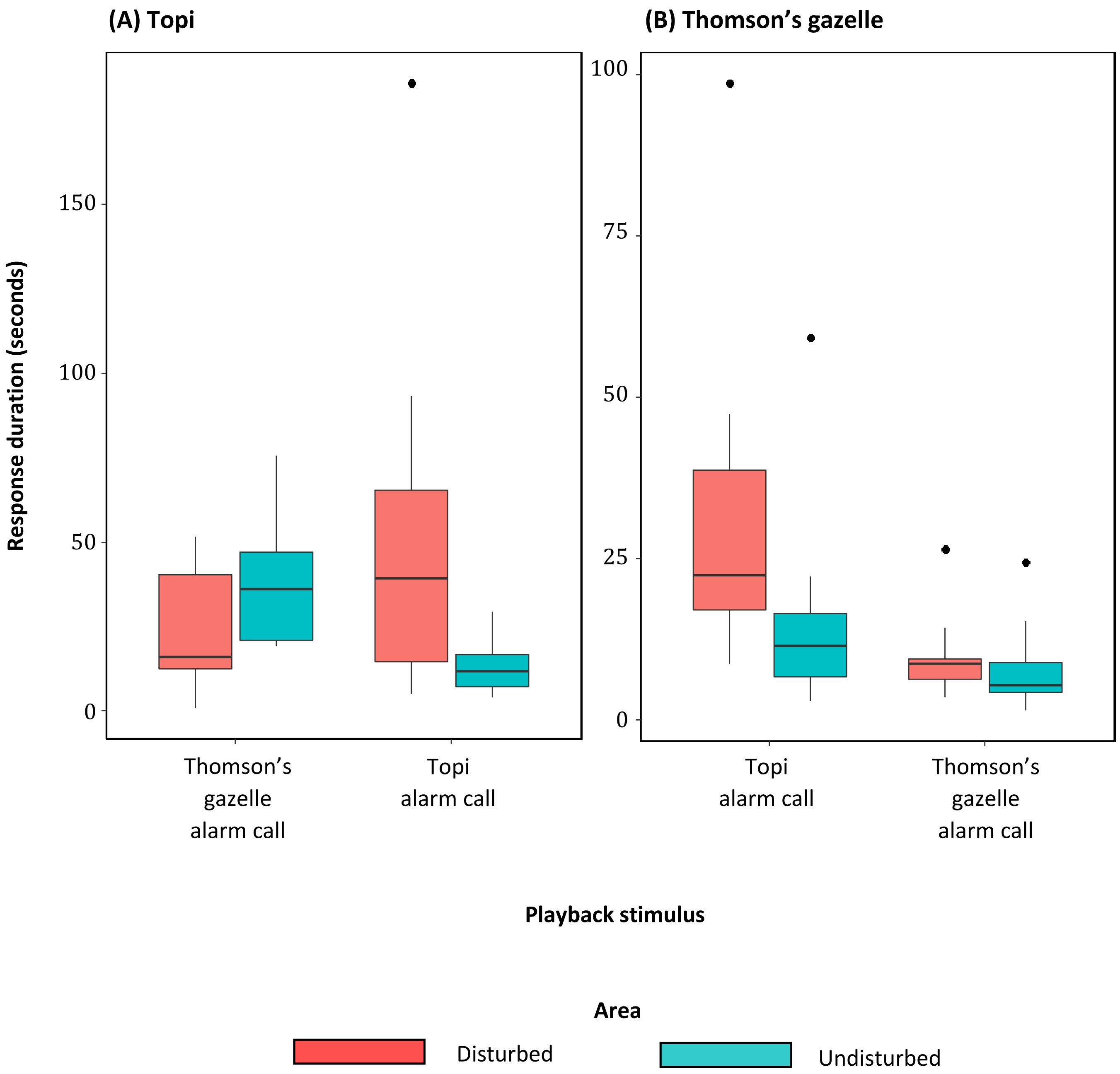


Figure 3: Response duration of topi (A) and Thomson's gazelle (B) to playbacks of conspecific and heterospecific alarm calls, in disturbed and undisturbed areas of the Maasai Mara National Reserve. Black dots represent outliers.

5.7 REFERENCES

Atickem, A., Loe, L. E., & Stenseth, N. C. (2014). Individual heterogeneity in use of human shields by mountain nyala. *Ethology*, **120**(7), 715-725.

Hansen, B. B., & Aanes, R. (2015). Habituation to humans in a predator-free wild ungulate. *Polar Biology*, **38**(2), 145-151.

Benítez-López, A. (2018). Animals feel safer from humans in the dark. *Science*, **360**(6394), 1185-1186.

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, **3**(6), 620-623.

Berger, J., Wangchuk, T., Briceno, C., Vila, A., & Lambert, J. E. (2020). Disassembled food webs and messy projections: modern ungulate communities in the face of unabating human population growth. *Frontiers in Ecology and Evolution*. In press.

Berger, J., Swenson, J. E., & Persson, I. L. (2001). Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science*, **291**(5506), 1036-1039.

Bhola, N., Ogutu, J. O., Piepho, H. P., Said, M. Y., Reid, R. S., Hobbs, N. T., & Olff, H. (2012). Comparative changes in density and demography of large herbivores in the Masai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya. *Biodiversity and Conservation*, **21**(6), 1509-1530.

Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication*. Sinauer.

Broekhuis, F., Madsen, E. K., & Klaassen, B. (2019). Predators and pastoralists: how anthropogenic pressures inside wildlife areas influence carnivore space use and movement behaviour. *Animal Conservation*, **22**(4), 404-416.

Broekhuis, F., Kaelo, M., Sakat, D. K., & Elliot, N. B. (2020). Human–wildlife coexistence: Attitudes and behavioural intentions towards predators in the Maasai Mara, Kenya. *Oryx*, **54**(3), 366-374.

Bro-Jørgensen, J. (2003). The significance of hotspots to lekking topi antelopes (Damaliscus lunatus). *Behavioral Ecology and Sociobiology*, **53**(5), 324-331.

Bro-Jørgensen, J., & Durant, S. M. (2003). Mating strategies of topi bulls: getting in the centre of attention. *Animal Behaviour*, **65**(3), 585-594.

Bro-Jørgensen, J., & Pangle, W. M. (2010). Male topi antelopes alarm snort deceptively to retain females for mating. *The American Naturalist*, **176**(1), 33-39

Butt, B. (2010). Seasonal space-time dynamics of cattle behavior and mobility among Maasai pastoralists in semi-arid Kenya. *Journal of Arid Environments*, **74**(3), 403-413.

Butt, B. (2014). The political ecology of'incursions': Livestock, protected areas and socio-ecological dynamics in the Mara region of Kenya. *Africa: Journal of the International African Institute*, 614-637.

Butt, B., & Turner, M. D. (2012). Clarifying competition: the case of wildlife and pastoral livestock in East Africa. *Pastoralism: Research, Policy and Practice*, **2**(1), 1-15.

Caro, T. M. (1994). Ungulate antipredator behaviour: preliminary and comparative data from African bovids. *Behaviour*, **128**(3), 189-228.

Caro, T. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press.

Caro, T. M., Lombardo, L., Goldizen, A. W., & Kelly, M. (1995). Tail-flagging and other antipredator signals in white-tailed deer: new data and synthesis. *Behavioral Ecology*, **6**(4), 442-450.

Carrasco, M. F., & Blumstein, D. T. (2012). Mule deer (*Odocoileus hemionus*) respond to yellow-bellied marmot (*Marmota flaviventris*) alarm calls. *Ethology*, **118**(3), 243-250.

Carthey, A. J., & Blumstein, D. T. (2018). Predicting predator recognition in a changing world. *Trends in Ecology & Evolution*, **33**(2), 106-115.

Ceballos, G., & Ehrlich, P. R. (2002). Mammal population losses and the extinction crisis. *Science*, **296**(5569), 904-907.

Ceppi, S. L., & Nielsen, M. R. (2014). A comparative study on bushmeat consumption patterns in ten tribes in Tanzania. *Tropical Conservation Science*, **7**(2), 272-287.

Cheney, D. L., & Seyfarth, R. M. (1992). *How monkeys see the world: Inside the mind of another species*. University of Chicago Press.

Ciuti, S., Muhly, T. B., Paton, D. G., McDevitt, A. D., Musiani, M., & Boyce, M. S. (2012a). Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B: Biological Sciences*, **279**(1746), 4407-4416.

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012b). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PloS One*, **7**(11), e50611.

Coleman, A., Richardson, D., Schechter, R., & Blumstein, D. T. (2008). Does habituation to humans influence predator discrimination in Gunther's dik-diks (*Madoqua guentheri*)?. *Biology Letters*, **4**(3), 250-252.

Cooke, S. J., Blumstein, D. T., Buchholz, R., Caro, T., Fernandez-Juricic, E., Franklin, C. E., & Wikelski, M. (2014). Physiology, behavior, and conservation. *Physiological and Biochemical Zoology*, **87**(1), 1-14.

Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, **25**(4), 773-784.

Crosmary, W. G., Makumbe, P., Côté, S. D., & Fritz, H. (2012). Vulnerability to predation and water constraints limit behavioural adjustments of ungulates in response to hunting risk. *Animal Behaviour*, **83**(6), 1367-1376.

Dröge, E., Creel, S., Becker, M., Christianson, D., M'Soka, J., & Watson, F. (2019). Response of wildebeest (*Connochaetes taurinus*) movements to spatial variation in long term risks from a complete predator guild. *Biological Conservation*, **233**, 139-151.

Durant, S. M., Caro, T. M., Collins, D. A., Alawi, R. M., & FitzGibbon, C. D. (1988). Migration patterns of Thomson's gazelles and cheetahs on the Serengeti Plains. *African Journal of Ecology*, **26**(4), 257-268.

Ekernas, L. S., Sarmento, W. M., Davie, H. S., Reading, R. P., Murdoch, J., Wingard, G. J., & Berger, J. (2017). Desert pastoralists' negative and positive effects on rare wildlife in the Gobi. *Conservation Biology*, **31**(2), 269-277.

Estes, R. D. (1991). *The behaviour guide to African mammals*. Halfway House.

Farr, M. T., Green, D. S., Holekamp, K. E., Roloff, G. J., & Zipkin, E. F. (2019). Multispecies hierarchical modeling reveals variable responses of African carnivores to management alternatives. *Ecological Applications*, **29**(2), e01845.

Favreau-Peigné, A., Calandreau, L., Constantin, P., Bertin, A., Arnould, C., Laurence, A., & Leterrier, C. (2016). Unpredictable and repeated negative stimuli increased emotional reactivity in male quail. *Applied Animal Behaviour Science*, **183**, 86-94.

FitzGibbon, C. D. (1989). A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Animal Behaviour*, **37**(3), 508-510.

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, **7**(11), 1325-1330.

Fryxell, J. M., & Berdahl, A. M. (2018). Fitness trade-offs of group formation and movement by Thomson's gazelles in the Serengeti ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**(1746), 20170013.

Funston, P. J., Mills, M. G. L., & Biggs, H. C. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, **253**(4), 419-431.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, **360**(6394), 1232-1235.

Geffroy, B., Samia, D. S., Bessa, E., & Blumstein, D. T. (2015). How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology & Evolution*, **30**(12), 755-765.

Gehr, B., Hofer, E. J., Muff, S., Ryser, A., Vimercati, E., Vogt, K., & Keller, L. F. (2017). A landscape of coexistence for a large predator in a human dominated landscape. *Oikos*, **126**(10), 1389-1399.

Green, D. S., Johnson-Ulrich, L., Couraud, H. E., & Holekamp, K. E. (2018). Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. *Biodiversity and Conservation*, **27**(4), 871-889.

Green, D. S., Zipkin, E. F., Incorvaia, D. C., & Holekamp, K. E. (2019). Long-term ecological changes influence herbivore diversity and abundance inside a protected area in the Mara-Serengeti ecosystem. *Global Ecology and Conservation*, **20**, e00697.

Greenberg, J. R., & Holekamp, K. E. (2017). Human disturbance affects personality development in a wild carnivore. *Animal Behaviour*, **132**, 303-312.

Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, **21**(1), 101-114.

Hunter, L. T. B., & Skinner, J. D. (1998). Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour*, **135**(2), 195-211.

Kassambara, A., Kosinski, M., Biecek, P., & Fabian, S. (2017). survminer: Drawing Survival Curves using'ggplot2'. *R package version 0.3*, *1*.

Kiffner, C., Peters, L., Stroming, A., & Kioko, J. (2015). Bushmeat consumption in the Tarangire-Manyara ecosystem, Tanzania. *Tropical Conservation Science*, **8**(2), 318-332.

Lowry, H., Lill, A., & Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, **88**(3), 537-549.

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews*, **90**(2), 560-586.

Margulies, J. D., & Karanth, K. K. (2018). The production of human-wildlife conflict: A political animal geography of encounter. *Geoforum*, **95**, 153-164.

Marion, S., Davies, A., Demšar, U., Irvine, R. J., Stephens, P. A., & Long, J. (2020). A systematic review of methods for studying the impacts of outdoor recreation on terrestrial wildlife. *Global Ecology and Conservation*, **22**, e00917.

Meise, K., Franks, D. W., & Bro-Jørgensen, J. (2018). Multiple adaptive and non-adaptive processes determine responsiveness to heterospecific alarm calls in African savannah herbivores. *Proceedings of the Royal Society B: Biological Sciences*, **285**(1882), 20172676.

Mogensen, N. L., Ogutu, J. O., & Dabelsteen, T. (2011). The effects of pastoralism and protection on lion behaviour, demography and space use in the Mara Region of Kenya. *African Zoology*, **46**(1), 78-87.

Mukeka, J. M., Ogutu, J. O., Kanga, E., & Røskaft, E. (2019). Human-wildlife conflicts and their correlates in Narok County, Kenya. *Global Ecology and Conservation*, **18**, e00620.

Nyhus, P. J. (2016). Human–wildlife conflict and coexistence. *Annual Review of Environment and Resources*, **41**.

Ogutu, J. O., Bhola, N., & Reid, R. (2005). The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *Journal of Zoology*, **265**(3), 281-293.

Okello, M. M. (2005). Land use changes and human–wildlife conflicts in the Amboseli Area, Kenya. *Human Dimensions of Wildlife*, **10**(1), 19-28.

Ordiz, A., Støen, O. G., Delibes, M., & Swenson, J. E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, **166**(1), 59-67.

Oriol-Cotterill, A., Valeix, M., Frank, L. G., Riginos, C., & Macdonald, D. W. (2015). Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, **124**(10), 1263-1273.

Owen-Smith, N. (2019). Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. *Biological Conservation*, **232**, 51-58.

Palmer, M. S., & Gross, A. (2018). Eavesdropping in an African large mammal community: antipredator responses vary according to signaller reliability. *Animal Behaviour*, **137**, 1-9.

Pangle, W. M., & Holekamp, K. E. (2010). Lethal and nonlethal anthropogenic effects on spotted hyenas in the Masai Mara National Reserve. *Journal of Mammalogy*, **91**(1), 154-164.

Paton, D. G., Ciuti, S., Quinn, M., & Boyce, M. S. (2017). Hunting exacerbates the response to human disturbance in large herbivores while migrating through a road network. *Ecosphere*, **8**(6), e01841.

Pelletier, F. (2006). Effects of tourist activities on ungulate behaviour in a mountain protected area. *Journal of Mountain Ecology*, **8**, 15-19.

Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., & Macdonald, D. W. (2012). Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*, **23**(5), 970-976.

Proffitt, K. M., Grigg, J. L., Hamlin, K. L., & Garrott, R. A. (2009). Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *The Journal of Wildlife Management*, **73**(3), 345-356.

R Development Core Team (2019). A language environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Sarmento, W., Biel, M., & Berger, J. B. J. (2016). Redistribution, human shields and loss of migratory behavior in the crown of the continent. *Intermountain Journal of Sciences*, **22**(4), 118-118.

Sarmento, W. M., & Berger, J. (2017). Human visitation limits the utility of protected areas as ecological baselines. *Biological Conservation*, **212**, 316-326.

Saltz, D., Berger-Tal, O., Motro, U., Shkedy, Y., & Raanan, N. (2019). Conservation implications of habituation in Nubian ibex in response to ecotourism. *Animal Conservation*, **22**(3), 220-227.

Schuttler, S. G., Parsons, A. W., Forrester, T. D., Baker, M. C., McShea, W. J., Costello, R., & Kays, R. (2017). Deer on the lookout: how hunting, hiking and coyotes affect white-tailed deer vigilance. *Journal of Zoology*, **301**(4), 320-327.

Seyfarth, R. M., & Cheney, D. L. (2010). Primate vocal communication. *Primate Neuroethology*, 84-97.

Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS One*, **9**(4), e94630.

Stabach, J. A., Wittemyer, G., Boone, R. B., Reid, R. S., & Worden, J. S. (2016). Variation in habitat selection by white-bearded wildebeest across different degrees of human disturbance. *Ecosphere*, **7**(8), e01428.

Therneau, T. M., & Lumley, T. (2014). Package 'survival'. *Survival analysis Published on CRAN*, *2*, 3.

Thompson, M. J., & Henderson, R. E. (1998). Elk habituation as a credibility challenge for wildlife professionals. *Wildlife Society Bulletin*, **20**, 477-483.

Treves, A., & Santiago-Ávila, F. J. (2020). Myths and assumptions about human-wildlife conflict and coexistence. *Conservation Biology*. In press.

Uchida, K., Suzuki, K. K., Shimamoto, T., Yanagawa, H., & Koizumi, I. (2019). Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behavioral Ecology*, **30**(6), 1583-1590.

Veldhuis, M. P., Ritchie, M. E., Ogutu, J. O., Morrison, T. A., Beale, C. M., Estes, A. B., & Wargute, P. W. (2019). Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. *Science*, **363**(6434), 1424-1428.

Walther, F. R. (1972). Territorial behaviour in certain horned ungulates, with special reference to the examples of Thomson's and Grant's gazelles. *African Zoology*, **7**(1), 303-307.

Walther, F. R., Mungall, C. E., & Grau, G.A. (1983). *Gazelles and their relatives: a study in territorial behaviour*. Noyes Publications. Park Ridge, New Jersey, USA.

Western, D., Nightingale, D. M., Mose, V. N., Sipitiek, J. O., & Kimiti, K. S. (2019). Variability and change in Maasai views of wildlife and the implications for conservation. *Human Ecology*, **47**(2), 205-216.

Wevers, J., Fattebert, J., Casaer, J., Artois, T., & Beenaerts, N. (2020). Trading fear for food in the Anthropocene: How ungulates cope with human disturbance in a multi-use, suburban ecosystem. *Science of The Total Environment*, 140369.

Wilmers, C. C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M. L., & Williams, T. (2013). Scale dependent behavioral responses to human development by a large predator, the puma. *PloS one*, **8**(4), e60590.

Young, J. K., Olson, K. A., Reading, R. P., Amgalanbaatar, S., & Berger, J. (2011). Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. *BioScience*, **61**(2), 125-132.

Zbyryt, A., Bubnicki, J. W., Kuijper, D. P., Dehnhard, M., Churski, M., & Schmidt, K. (2018). Do wild ungulates experience higher stress with humans than with large carnivores?. *Behavioral Ecology*, **29**(1), 19-30.

5.8 APPENDIX

Differences in social and ecological variables according to the level of human disturbance

I tested for differences in socio-ecological variables between disturbed and undisturbed areas using Wilcoxon rank-signed tests. I found no significant differences in group size (W = 1135.5, p = 0.7713), distance to cover (W = 968.5, p = 0.1352), and wind speed (W = 1300.5, p = 0.368). Grass was conversely taller in undisturbed rather than disturbed areas (W = 588, p < 0.0001). This means that, except for grass height, the variation in environmental conditions was similar between disturbed and undisturbed areas, and thus unlikely to confuse the over-arching effects of human disturbance on the responses to playback stimuli.

Correlations of alarm call responsiveness with socio-ecological variables

Potential effects of socio-ecological variables on response strength were explored by applying Spearman's rank correlation tests. In both topi and gazelles, there were no significant correlations between the response latency to conspecific alarm calls and: distance to the focal individual (topi: z = 0.696, p = 0.487; gazelle: z = 1.494, p = 0.135), group size (topi: z = 0.555, p = 0.344; gazelle: z = -0.425, p = 0.671), distance to cover (topi: z = - 0.05, p = 0.960; gazelle: z = 1.645, p = 0.100), and wind speed (topi: z = 0.548, p = 0.584; gazelle: z = - 0.805, p = 0.421). Similar results were found for latency to respond to heterospecific alarm calls, with no significant correlations with distance to focal individual (topi: z = 0.667, p = 0.498; gazelle: z = 0.903, p = 0.366), group size (topi: z = 0.963, p = 0.335; gazelle: z = 0.538, p = 0.590), distance to cover (topi: z = 0.091, p = 0.927; gazelle: z = 0.198, p = 0.843), and wind speed (topi: - 1.795, p = 0.274; gazelle: z = - 0.850, p = 0.395).

I found no significant correlations, for the two study species, between response duration to conspecific alarm calls and distance to focal individual (topi: z = 0.133, p = 0.825; gazelle: z = 0.025, p = 0.98), group size (topi: z = - 0.605, p = 0.545; gazelle: z = 1.196, p = 0.232), distance to cover (topi: z = 0.596, p = 0.551; gazelle: z = - 1.218, p = 0.223), and wind speed (topi: z = -0.597, p = 0.551; gazelle: z = 0.025, p = 0.58). The same was true for responses to heterospecific alarm calls, which were not correlated with distance to focal individual (topi: z = 0.58, p = 0.627; gazelle: z = - 1.383, p = 0.167), group size (topi: z = 0.050, p = 0.950; gazelle: z = 0.737, p = 0.461), distance to cover (topi: z = 0.23, p = 0.818; gazelle: z = - 0.678, p = 0.498), and wind speed (topi: z = 0.747, p = 0.455; gazelle: z = 0.651, p = 0.515).

Correlations of alarm call responsiveness with grass height

I observed stronger responses of topi and gazelles to conspecific alarm calls at playback sites with shorter grass. In particular, the response latency of topi to conspecific alarm calls was positively correlated with grass height, corresponding to longer times to become alert in areas of tall grass (z = 2.289, p = 0.022). Such correlations were however not significant for gazelles (z = 0.399, p = 0.690). In both species, response duration to conspecific alarm calls was negatively associated with grass height, meaning that individuals remained alert for longer in short grass (topi: z = - 2.434, p = 0.015; gazelle: z = - 2.511, p = 0.012). By contrast, the intensity of the reactions to heterospecific alarm calls was not significantly correlated with grass height, neither for response latency (topi: z = - 0.743, p = 0.458; gazelle: z = 0.952, p = 0.366), nor for response duration (topi: z = 0.46, p = 0.560; gazelle: z = 0.311, p = 0.756).

These results imply that: (i) alarm call responsiveness was counter-intuitively weaker at sites with taller rather than shorter grass, despite the greater vulnerability to predation risk for antelopes (Caro 1994; Kitchen et al. 2010; Meise et al. 2018); and that (ii) the observed patterns were inexplicably restricted to playbacks of conspecifics. The most likely explanation is that these correlations were spurious: they simply reflected a heightened responsiveness to conspecific alarm calls in disturbed areas, where grass was consistently shorter than in undisturbed areas. Further evidence comes from the lack of an association between gazelle response latency to conspecific alarm calls and grass height: this closely reflected the non-significant difference on this behavioural measure between disturbed and undisturbed areas (see the Results section). Similarly, responses to heterospecific alarm calls were also not affected by the level of human disturbance, and again did not show any significant correlations with grass height. The observed variation in the responsiveness to conspecific alarm calls between disturved and undisturbed areas could therefore be attributed to differences in the level of anthropogenic interference with antipredator behaviour, not in grass height.

References

Caro, T. M. (1994). Ungulate antipredator behaviour: preliminary and comparative data from African bovids. *Behaviour*, **128**(3), 189-228.

Kitchen, D. M., Bergman, T. J., Cheney, D. L., Nicholson, J. R., & Seyfarth, R. M. (2010). Comparing responses of four ungulate species to playbacks of baboon alarm calls. *Animal Cognition*, **13**(6), 861-870.

Meise, K., Franks, D. W., & Bro-Jørgensen, J. (2018). Multiple adaptive and non-adaptive processes determine responsiveness to heterospecific alarm calls in African savannah herbivores. *Proceedings of the Royal Society B: Biological Sciences*, **285**(1882), 20172676.

CHAPTER 6: GENERAL CONCLUSIONS

In this final chapter I provide a summary of my key findings, and of possible future lines of research that could be pursued. The main goal of this thesis is to further our current understanding of the ultimate and proximate drivers of complexity, diversity, and flexibility in ungulate visual and acoustic signals. In Chapter 2-4 I tested the validity of multiple adaptive hypotheses advanced to explain the adaptive significance of elaborate sexual signalling systems (namely gestural displays, morphological ornaments, and complex vocalizations), using both comparative analyses and playback experiments in the field. In Chapter 5, I addressed the impact of human disturbance on the plasticity of ungulate antipredator signalling systems. There are several implications for the conservation of wild ungulates emerging from the results of each chapter, which are discussed below.

Mating strategies and sexual signals (Chapter 2 and Chapter 3)

My comparative analyses suggest that the strategies adopted by male ungulates to secure mating opportunities is of key importance for the evolution of both behavioural and morphological sexual signals. Specifically, male non-territoriality appears as a strong promoter of highly elaborate gestural courtship displays in bovids and cervids (Chapter 2), and of exaggerated sexual dimorphism in morphological traits such as colourations and pelage ornaments in bovids (Chapter 3). By contrast, species adopting territorial mating strategies exhibit smaller repertoires of gestural courtship displays, and less pronounced morphological dimorphism. Although these patterns may be explained mainly by the smaller potential for polygyny in territorial systems (i.e. oestrous females are shared among territorial males), such an interpretation is not always applicable. For example, some territorial ungulates which are highly polygynous exhibit simpler courtship displays and a smaller magnitude of dimorphism than non-territorial species which accrue lower levels of polygyny (i.e. forming smaller breeding groups). I here propose that sexual selection might target different male traits according to the mating strategy. In particular, since territories provide references to male quality and competitive ability, this might attenuate the drive for individual-based gestural displays and ornaments. Additional research is now warranted to determine whether the role of territories as “extended sexual phenotypes” could effectively modify the operation of sexual selection in bovids and cervids.

Species recognition as a driver of courtship display complexity (Chapter 2)

The results in Chapter 2 show that the complexity of gestural courtship displays in male bovids and cervids is positively correlated with the number of closely-related species living in sympatry. I suggest that these patterns genuinely reflect a causal connection: the costs associated with hybridization risk in contexts where several species co-exist might have driven larger display repertoires, facilitating diversification and thus the recognition of conspecifics during courtship. This is in agreement with previous authors (e.g. Freeberg, Dunbar & Ord 2012; Hill 2015), who theorized that sexual signals would become more elaborate in species-rich communities, under selection pressures for hybridization avoidance. Despite ample theoretical support for this hypothesis, comparative-based evidence has been relatively scarce until now. My findings thus open up the possibility for further explorations of species recognition as a promoter of signal complexity.

Mixed-sex herds and sexual dimorphism (Chapter 3)

One of my most intriguing findings is that social integration in mixed-sex herds seemingly counter-acts the positive drive of sexual selection towards the evolution of dimorphic morphological traits in male bovids. This hypothesis has been circulating among behavioural ecologists for more than 40 years (with slightly different formulations: Geist 1974; Jarman 1983; Estes 1991, 2000), but lacked robust statistical testing. In Chapter 3, I reveal a strong negative correlation between bovid sexual aggregation (i.e. the propensity to join social groups containing multiple males and females), and sexual dimorphism in colour and pelage ornaments, providing the first comparative evidence of the social integration hypothesis. My interpretation is that morphological dimorphism is inherently costly in mixed-sex herds, most notably because it amplifies male exposure to predation risk due to oddity effects. Ornamented males would be very conspicuous and easily targeted by visually-oriented predators in mixed-sex herds: such high survival costs might have thus prevented the acquisition of dimorphic visual traits, including contrasting colourations and flamboyant hair structures such as beards or manes. My explanation based on oddity effects however requires further confirmation from field studies. For example, one could focus on dimorphic species which are seasonally or occasionally aggregated in mixed-sex herds (e.g. eland *Taurotragus oryx*, saiga *Saiga tatarica*, and white-eared kob *Kobus kob leucotis*), and compare the rates of predation on ornamented males in male-female versus male-only herds. Alternatively, individuals in mixed-sex herds could also be equipped with artificial “ornaments” in order to quantify the potential for odd appearances to attract predators (pending ethical considerations).

Alarm call co-option and the evolution of complex vocal displays (Chapter 4)

My results in Chapter 4 show that the snorting component of male impala roaring displays is equivalent to the alarm snort emitted upon detecting predators. To my knowledge, this is the first evidence to date that a pre-existing alarm call can be included as part of a complex vocal display of sexual-aggressive advertisement. The outcome of playback trials also indicates that the presence of snorts in roaring displays shortens the latency of male impala to respond aggressively to the following grunting calls (the other component of the display), thus suggesting that snorting serves an attention-grabbing function. Additional research is now required to determine which selective advantages could derive from the co-option of snorts into roaring displays. For example, direct observations of male impala agonistic behaviour could clarify the costs associated with producing grunting calls (i.e. the energetics associated with the lowering of the larynx), and if these are found to be considerable, this may explain the benefits prefixing grunts with snorts to enhance signal efficacy. The information content of the grunts also warrants further investigation.

My findings could also lead the way for the exciting opportunity to investigate the evolutionary drivers of alarm call co-option into complex vocal displays at a broader phylogenetic scale. Analogies with the impala roaring display can be found in a variety of mammals, and are not limited to ungulates. One striking similarity, for example, is offered by the multi-component utterances of the black-and-white colobus monkey: the male aggressive roars (which advertise territorial occupancy) are usually preceded by short, explosive “snorts”, sounding identical to those emitted in response to approaching leopards (Marler 1972). The playback experimental framework described in Chapter 4 could therefore be applied to identify whether or not the alarm calls in the elaborate vocalizations of the colobus monkey and of other species also correspond to attention-grabbing display components.

Human impacts on ungulate antipredator signalling systems (Chapter 5)

My results in Chapter 5 show that human disturbance can substantially alter ungulate antipredator signalling systems. Specifically, I found that topi and Thomson’s gazelles in the Maasai Mara National Reserve (Kenya) exhibited heightened responsiveness to playbacks of conspecific alarm calls in areas closer to human settlements. This contrasted with my expectation that the shielding effect against natural predation risk provided by anthropogenic activities would have reduced individual exposure to alarm calls and thus attenuated response intensities. I propose that, although human disturbance does deter natural predators from settled areas, alarm calling might have become associated with unpredictable, but infrequent, anthropogenic threats which demand careful assessment by wild ungulates.

This interpretation needs additional research. Observational studies might provide a more detailed understanding of why anthropogenic threats might require a greater degree of attention by antelopes than those posed by large carnivores. One possible approach could be to quantify the reactions of topi and gazelles to various types of stimuli associated with human disturbance, and to the reactions elicited by natural predators. Also, similar studies in other taxa and locations may provide insights into the generality of my “human unpredictability hypothesis”.

Implications for ungulates conservation

The results discussed in this thesis have several implications for ungulates conservation. The comparative analyses in Chapter 2 and Chapter 3 emphasize the remarkable interspecific variability in the shape and elaboration of ungulate gestural courtship displays and ornaments. Such diversity demands dedicated conservation efforts, as the extinction of single species would translate into the loss of unique behavioural and morphological phenotypes. Although conserving behaviour is a relatively new idea in conservation biology (Whitehead 2010; Greggor et al. 2016, it is increasingly regarded a crucial element for the successful preservation of long-term evolutionary processes (Saether & Engen 2019; Carthey et al. 2020). Effective conservation strategies should therefore focus not only on ensuring the viability of wild ungulate populations, but also on promoting the long-term persistence of adaptive variation in signalling traits.

The results from my playback experiments on male impala (Chapter 4) stress the importance of ungulates as a model system for the study of acoustic communication. Deciphering the “meaning” of elaborate vocalizations in impalas and other antelopes might provide novel insights into the functional value of call combinations, and enable comparisons with the signalling behaviour of other mammals and even with human language. The conservation of wild ungulates, including those species which are relatively common (impalas are classified as “Least Concern” by the IUCN), should therefore be prioritized by wildlife managers not only on ecological grounds, but also as an asset for evolutionary biologists to explore the ultimate drivers of complexity in animal and human communication.

The results presented in Chapter 5 provide insights that may potentially be useful for the management of ungulates in protected areas. The heightened alarm call responsiveness of topi and gazelles along the boundary of the reserve indicates that human disturbance might be exacerbating the time devoted to risk-sensitive behaviours, with potentially deleterious effects on population performance. These two species have been rapidly declining in local densities across the entire Serengeti-Mara ecosystem over the past three decades (Ogutu et al. 2009, 2011). Although such declines can be largely attributed to rangeland degradation (Ogutu et al. 2011), my findings suggest that fear-mediated anthropogenic impacts on activity patterns and energy budgets may also be a contributing factor.

My research endeavours ultimately suggest that behavioural ecology should not be neglected while planning for the conservation and management of wild ungulate populations. An improved understanding of animal communication systems may indeed offer useful insights to conservationists, and help us understand how human impacts on behaviour alter ecological functionality. Finally, it is my hope that this thesis will ignite scientific curiosity and prompt renewed attention to the preservation of ungulates and of their environment.

6.1 REFERENCES

Carthey, A. J., Blumstein, D. T., Gallagher, R. V., Tetu, S. G., & Gillings, M. R. (2020). Conserving the holobiont. *Functional Ecology*, **34**(4), 764-776.

Estes, R. D. (1991b). The significance of horns and other male secondary sexual characters in female bovids. *Applied Animal Behaviour Science*, *29*(1), 403-451.

Estes, R. D. (2000). Evolution of conspicuous coloration in the Bovidae: female mimicry of male secondary sexual characters as a catalyst. In Schaller, G.B., & Vrba, E. S. (Eds). *Antelopes, deer and relatives*. Yale University Press, New Haven & London.

Freeberg, T. M., Dunbar, R. I., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 1785-1801.

Geist, V. (1974). On the relationship of social evolution and ecology in ungulates. *American Zoologist*, **14**(1), 205-220.

Greggor, A. L., Berger-Tal, O., Blumstein, D. T., Angeloni, L., Bessa-Gomes, C., Blackwell, B. F., & Goldenberg, S. Z. (2016). Research priorities from animal behaviour for maximising conservation progress. *Trends in Ecology & Evolution*, **31**(12), 953-964.

Hill, G. E. (2015). Sexiness, individual condition, and species identity: the information signaled by ornaments and assessed by choosing females. *Evolutionary Biology*, **42**(3), 251-259.

Jarman, P. (1983). Mating system and sexual dimorphism in large terrestrial, mammalian herbivores. *Biological Reviews*, **58**(4), 485-520.

Marler, P. (1972). Vocalizations of East African monkeys II: black and white colobus. *Behaviour*, **42**(3-4), 175-197.

Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., & Reid, R. S. (2009). Dynamics of Mara–Serengeti ungulates in relation to land use changes. *Journal of Zoology*, **278**(1), 1-14.

Ogutu, J. O., Owen‐Smith, N., Piepho, H. P., & Said, M. Y. (2011). Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. *Journal of Zoology*, **285**(2), 99-109.

Sæther, B. E., & Engen, S. (2019). Towards a predictive conservation biology: the devil is in the behaviour. *Philosophical Transactions of the Royal Society B*, **374**(1781), 20190013.

Whitehead, H. (2010). Conserving and managing animals that learn socially and share cultures. *Learning & Behavior*, **38**(3), 329-336.