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„Social Behaviour and Movement Ecology of the Northern Bald Ibis (*Geronticus eremita*): Contributions to the Behavioural Ecology of an Endangered Avian Species“

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This thesis is based on the following papers:

PART I

Physiological implications of social behaviour

CHAPTER I

Puehringer-Sturmayr V, Wascher CAF, Loreto M-C, Palme R, Stoewe M, Kotrschal K, Frigerio D (2018) Seasonal differences of corticosterone metabolite concentrations and parasite burden in northern bald ibis (*Geronticus eremita*): The role of affiliative interactions. PLoS ONE 13(1): e0191441

CHAPTER II

Puehringer-Sturmayr V, Stiefel T, Kotrschal K, Kleindorfer S, Frigerio D (2021) Social interactions change with season and age in Northern Bald Ibis. Journal of Ornithology 162: 277-288

PART II

Movement ecology in social animals

CHAPTER III

Puehringer-Sturmayr V, Loretto M-C A, Hemetsberger J, Czerny T, Gschwandegger J, Leitsberger M, Kotrschal K, Frigerio D (2020) Effects of bio-loggers on behaviour and corticosterone metabolites of Northern Bald Ibises (*Geronticus eremita*) in the field and in captivity. Animal Biotelemetry 8: 2

The data discussed in **Chapter III** were also published in the Journal ‘Frontiers for Young Minds: Science for kids, edited by kids’, an open-access scientific journal written by scientists and reviewed by a board of kids and teens.
Puehringer-Sturmayr V, Hemetsberger F, Frigerio D (2020) Tracking birds: How a little backpack could affect the life of a wild bird. Frontiers for Young Minds 8: 116

CHAPTER IV

Puehringer-Sturmayr V, Krejci J, Schuster R, Kleindorfer S, Kotrschal K, Frigerio D, Loretto M-C. Space use and site fidelity in the endangered Northern Bald Ibis (*Geronticus eremita*): Effects of age, season and sex. Bird Conservation International. Manuscript ID: BCI-MP-2021-0010. In resubmission

Picture credit: Verena Pühringer-Sturmayr

It seems to me that the natural world is
the greatest source of excitement;
the greatest source of visual beauty;
the greatest source of intellectual interest.
It is the greatest source of so much in life that makes life worth living.

David Attenborough

CONTENTS

ABSTRACT

This thesis investigates (1) the relationship between social behaviour and physiology, and (2) the factors that shape space use patterns in the endangered Northern Bald Ibis (NBI, *Geronticus eremita*). The reproductive season is energetically costly, often resulting in up-regulated glucocorticoid secretion and constrained immune functions. **Chapter I** discusses the role of affiliative behaviour in corticosterone metabolite excretion and endoparasite burden, while **Chapter II** analyses factors affecting social relationships. Social relationships can be modulated by the environment, but social, individual and abiotic factors can also alter space use, which is addressed in **Chapter IV**. However, to ensure observation of natural behaviour, assessing potential effects of GPS transmitters on social behaviour and physiology is critical (**Chapter III**). The more significant findings to emerge are that (1) NBI appear to buffer endoparasite burden through affiliative interactions during periods of elevated glucocorticoid secretion, (2) social connections seem to increase with age, which could impact juvenile recruitment and reintroduction projects, (3) GPS-tagged birds had increased glucocorticoid levels one month after being tagged, and (4) NBI were found to be fairly consistent in their use of space. In conclusion, these findings (1) indicate that affiliative interactions may positively affect immune functions and alleviate endoparasite burden, (2) can be used to protect the most important areas for this species, such as foraging and roosting areas, and (3) suggest that younger birds may face higher rates of mortality and dispersal as a result of having fewer social connections.

GERMAN ABSTRACT/ZUSAMMENFASSUNG

Ziel dieser Arbeit war es, zwei Aspekte der Verhaltensökologie des gefährdeten Waldrapps (*Geronticus eremita*) zu untersuchen: (1) die Synergie von Sozialverhalten und Physiologie und (2) die Auswirkungen individueller und abiotischer Faktoren auf die Raumnutzungsmuster. Die Fortpflanzungszeit ist energetisch kostspielig und führt häufig zu einer erhöhten Ausschüttung von Glukokortikoiden und eingeschränkten Immunfunktionen. In **Kapitel I** wird die Rolle von sozio-positiven Verhalten bei der Ausscheidung von Kortikosteron-Metaboliten und der Belastung durch Endoparasiten erörtert, während in **Kapitel II** Faktoren analysiert werden, die sich auf soziale Beziehungen auswirken. Soziale Beziehungen können durch die Umwelt moduliert werden, aber auch soziale, individuelle und abiotische Faktoren können die Raumnutzung verändern, was in **Kapitel IV** behandelt wird. Um die Beobachtung natürlicher Verhaltensweisen zu gewährleisten, ist jedoch die Beurteilung potenzieller Auswirkungen von GPS-Sendern auf das Sozialverhalten und die Physiologie von entscheidender Bedeutung (**Kapitel III**). Die wichtigsten Ergebnisse sind, dass (1) Waldrappe in Zeiten erhöhter Ausschüttung von Glukokortikoiden die Belastung durch Endoparasiten durch sozio-positive Interaktionen abzufedern scheinen, (2) soziale Bindungen mit dem Alter zuzunehmen scheinen, was sich auf die Rekrutierung von Jungvögeln und Wiederansiedlungsprojekte auswirken könnte, (3) mit GPS-Sendern versehene Vögel einen Monat nach der Ausstattung erhöhte Glukokortikoidspiegel aufweisen und (4) Waldrappe in ihrer Raumnutzung ziemlich konsistent sind. Zusammenfassend lässt sich sagen, dass diese Ergebnisse (1) darauf hindeuten, dass sich sozio-positive Interaktionen positiv auf die Immunfunktionen auswirken und die Belastung durch Endoparasiten verringern können, (2) zum Schutz der wichtigsten Gebiete für diese Art, wie beispielsweise Futter- und Schlafplätze, genutzt werden können und (3) darauf hindeuten, dass jüngere Vögel aufgrund geringerer sozialer Bindungen mit einer höheren Sterblichkeits- und Verbreitungsrate konfrontiert sein könnten.

SYNOPSIS

The aim of this thesis is to investigate two aspects of behavioural ecology – social behaviour and movement ecology – during the breeding and non-breeding season in the Northern Bald Ibis (*Geronticus eremita*), an endangered bird species. My research focused on the link between social behaviour and physiology and the influence of individual and abiotic factors on space use and site fidelity patterns. I chose the Northern Bald Ibis as study species not only because of its conservation status, but also because Northern Bald Ibis are group-living and highly social birds.

In **Chapter I** and **Chapter III**, I validated the following methods used in the subsequent chapters: (1) I tested which enzyme immunoassay is most appropriate for non-invasive measurements of excreted corticosterone metabolite concentrations in Northern Bald Ibis, which is an essential step for proper interpretation of hormone metabolite concentrations and (2) I tested the feasibility of using GPS transmitters in Northern Bald Ibis and whether and to what extent they affect behavioural and physiological parameters. I discovered that the enzyme immunoassay ’11-oxoaetiocholanolone’ was the best-suited assay. In comparison to other assays tested, this assay was more sensitive and detected peaks in excreted corticosterone metabolite concentrations for longer periods. Furthermore, GPS transmitters had no effect on maintenance behaviour (i.e. preening, scratching, shaking, stretching, bathing), dorsal feather preening, locomotion, and foraging. However, affiliative interactions in tagged individuals decreased directly after tagging and excreted corticosterone metabolite concentrations were still elevated one month after tagging, but returned to baseline levels shortly thereafter.

The reproductive season is socially and energetically costly, often resulting in increased glucocorticoid secretion and constrained immune functions. Social allies may help buffer physiological stress responses, thereby benefitting immune functions and reducing parasite burden. In **Chapter I**, I investigated whether affiliative behaviour modulates excreted corticosterone metabolite levels and endoparasite burden during the breeding and non-breeding season. I found higher excreted corticosterone metabolite levels and more droppings containing endoparasite products during the reproductive season than during the post-reproductive one. Paired individuals had lower endoparasite burden, increased corticosterone metabolite concentrations and initiated affiliative interactions more frequently than unpaired birds. In **Chapter II**, I examined the effect of season, sex, age, and reproductive partner on social interactions. Here, I found seasonal differences in proximity patterns and affiliative behaviour, with higher proximity and less affiliative interactions during autumn than winter. Females received more affiliative behaviour compared to males. Reproductive partners were preferred affiliative interaction partners, and central social positions were age-specific, with older birds occupying more central positions. This is the first study to investigate social networks in Northern Bald Ibis, which may be used to adapt conservation actions by tracking social relationships between individuals and consequently the transmission risk of parasite load.

Social behaviour and physiology studies combined with movement analyses can further address questions regarding the vulnerability of a population. Space use patterns are closely linked to survival. Individuals often return to specific areas and may develop site fidelity in habitats supporting survival and/or reproductive success, which may constrain optimal choice of habitat and favour conservative habitat use. But, little is known about the movement ecology of Northern Bald Ibis in terms of reproductive and individual differences. In **Chapter IV**, I investigated whether sex, age class, and season affect space use and site fidelity patterns. I discovered consistently high site fidelity and overlapping space use between individuals over successive years. Individuals used consistent flyways along valleys rather than mountainous areas when flying between areas. Furthermore, adults had more expansive space use during the breeding season than during the non-breeding season, while I only observed a slight change in juveniles. Adults also showed higher site fidelity compared to juveniles. Yet, no sex differences were found.

With this thesis, I contribute to the field of behavioural ecology by enhancing the understanding of the role of affiliative behaviour in stress response, factors influencing social relationships and individual social position within a group, the role of male affiliative behaviour in pair formation, age-related mortality risk associated with different social network positions, the importance of physiological effects of GPS-transmitters, and the link between seasonal trends in habitat use and behaviour. The most important findings of this theses are that affiliative interactions in Northern Bald Ibis seem to buffer endoparasite burden during periods of up-regulated glucocorticoid secretion, individuals were found to be rather consistent in their space use patterns, and younger individuals had fewer social connections, which could impact recruitment and reintroduction projects. In conclusion, these findings (1) suggest that being well embedded in a pair bond may positively affect immune function and parasite burden, (2) can be used to conserve existing foraging and roosting areas that are frequently used, and (3) younger individuals may face higher mortality and dispersal rates due to occupying less socially central positions. Taken together, these findings could inform conservation to generate new or improve existing strategies for the endangered Northern Bald Ibis.

GENERAL INTRODUCTION

Currently, approximately 40% of the world's bird populations are declining, mainly due to agriculture, logging, hunting, invasive species and climate change (BirdLife International 2018b; Rosenberg *et al.* 2019), stressing the need to inform conservation management and develop new or advance existing conservation strategies. Behavioural ecology is closely linked to conservation and investigates behavioural strategies that affect survival and reproduction (and consequently recruitment), thereby providing information on population and community dynamics as well as causes for evolutionary behavioural adaptations, habitat characteristics, and environmental and evolutionary changes by combining three behavioural domains: (1) social behaviour and reproduction, (2) movement and space-use patterns, and (3) foraging and predator-prey related behaviours (Berger-Tal *et al.* 2011). All three behavioural domains can be used to inform conservation management about the vulnerability of a species, the state of their habitat, survival and reproduction based on conclusions about behavioural physiology, social network, habitat selection, and home range use (Morris *et al.* 2009).

My PhD thesis focuses on the first two behavioural domains and is composed of two parts, which aim at a better understanding of (1) the physiological implications (i.e. excreted corticosterone metabolite concentrations and endoparasite burden) of social behaviour (specifically affiliative behaviour) and (2) movement ecology of social animals (i.e. space use patterns and site fidelity). Thereby, these findings generate biologically relevant conclusions in regard to the behavioural ecology of the Northern Bald Ibis (*Geronticus eremita*), an endangered species and still one of the most threatened avian species worldwide, and can inform conservation management.

STUDY SPECIES:
THE NORTHERN BALD IBIS, *GERONTICUS EREMITA*

Over the last century Northern Bald Ibis (*Geronticus eremita*) populations dwindled and many colonies disappeared from most of their former range (Bowden *et al.* 2003), leaving only about 700 individuals in the wild in the Souss-Massa National Park colony in Morocco (Africa; assessed in August 2018, Oubrou & Bekkay 2018). In the 20th century, however, colonies were widespread throughout Algeria, Turkey and Syria (Figure 1; Böhm *et al.* 2020).

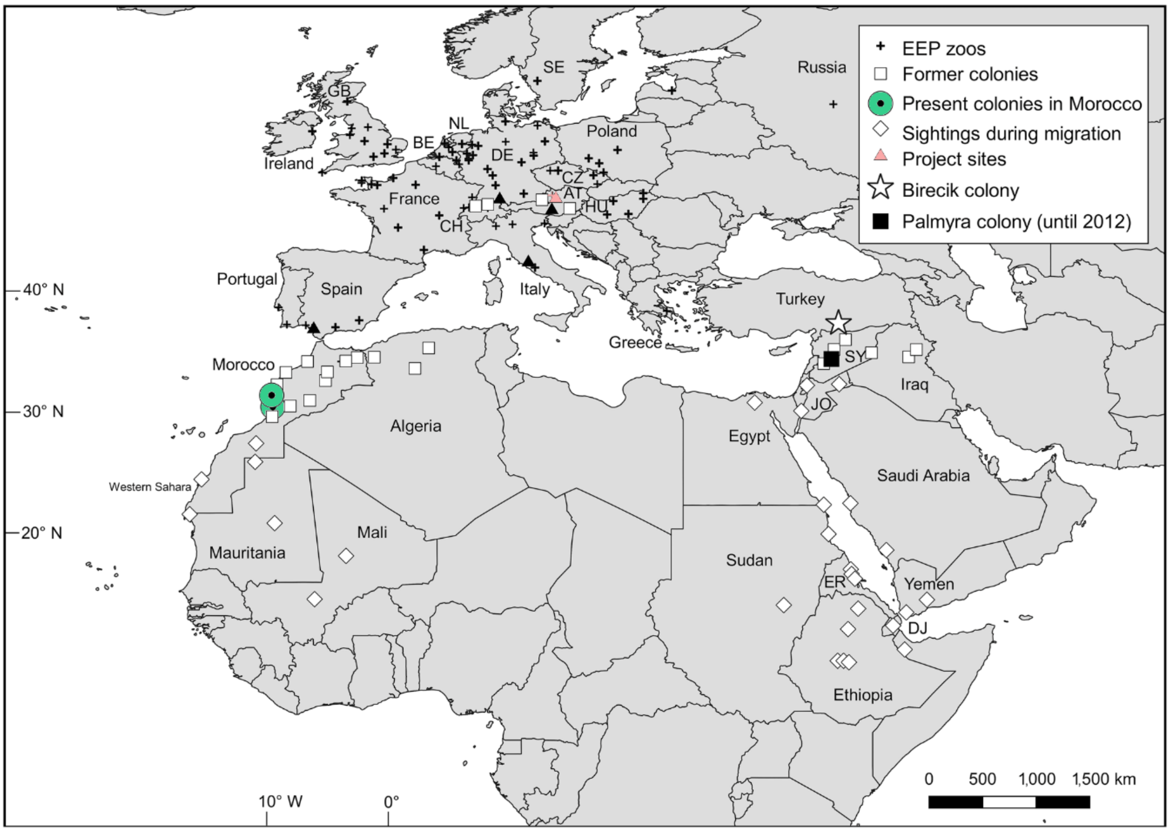

Figure 1. Former and present distribution range of the Northern Bald Ibis. Present colonies in Morocco are marked in green, the study area at the Konrad Lorenz Research Center in Austria is marked in pink. Adapted from Böhm *et al.* (2020), p. 2, accessed 20 February 2021.

Despite intense and committed conservation and rehabilitation initiatives, e.g. by the Konrad Lorenz Research Center for Behavior and Cognition (a Core Facility of the University of Vienna, Austria), the Waldrappteam (Austria/Germany, LIFE+

project “Reason for Hope – Reintroduction of the Northern Bald Ibis in Europe”, Fritz 2004), the Projecto Eremita (Spain) and other members of the International Advisory Group for the Northern Bald Ibis (IAGNBI, http://www.iagnbi.org/, supported by the RSPB – Royal Society for the Protection of Birds, BirdLife International and the WWF), the Northern Bald Ibis is still considered one of the most endangered bird species in the world (BirdLife International 2018a). The main factors leading to the disappearance from its former range are habitat destruction, persecution and the influence of agricultural pesticides (Collar *et al.* 1985; Hirsch 1976, 1979). Furthermore, Northern Bald Ibis seem rather consistent in habitat use and foraging sites (Kirnbauer 2004; Serra *et al.* 2008), indicating that site fidelity may play a major role in selecting foraging habitats. This has also been suggested as a reason for the decline of the species throughout its original distribution range. Thus, in case of endangered species such conservativism may increase the risk of population decline. In addition, environmental conditions, such as very dry years, evidently had an impact on the breeding success of the Moroccan population. Individuals had to undergo long distance flights from the breeding colony to fresh water sources and low rainfall consequently led to low prey availability. However, when provided with supplementary fresh water sources, reproductive success increased, buffering the impact of low rainfall (Smith *et al.* 2008). Conservation actions and management of the Moroccan population has led to an increase in the natural wild population (Böhm *et al.* 2020), leading to a recategorization of the conservation status from ‘critically endangered’ to ‘endangered’ in 2018 (BirdLife International 2020; Figure 2).

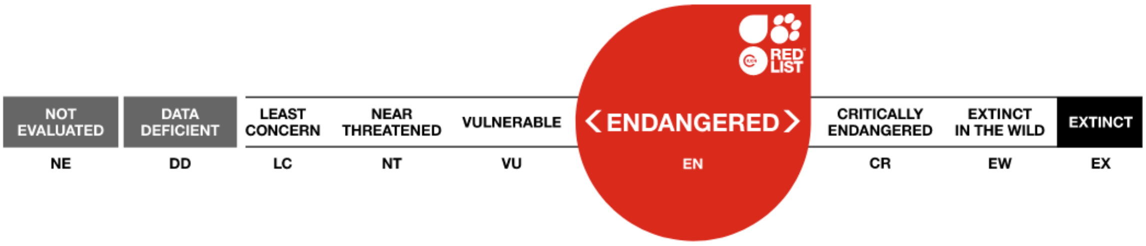

Figure 2. Red list category of the Northern Bald Ibis. Reprinted from BirdLife International (2018a), accessed 01 June 2021.

The Northern Bald Ibis is a year-round colonial, highly social, and seasonal monogamous avian species, which breeds in dense colonies (e.g. on sandstone cliffs in their natural habitat) and forages in flocks of different sizes. Individuals show biparental care (Böhm & Pegoraro 2011). In general, the strength of pair bonds in seasonally monogamous species changes with the reproductive cycle (Rowley & Bateson 1985), which can also be observed in the Northern Bald Ibis, which has strong pair bonds during the breeding season and looser bonds during the non-breeding season. Further descriptions of the biology, social behaviour and movement patterns of the Northern Bald Ibis are indicated in **Chapter I**, **II** and **IV**.

Studies on the Moroccan Northern Bald Ibis population showed that they prefer dry steppe-like habitats with sparse cover of perennial and annual vegetation, cultivation, and two-year fallows (Bowden *et al.* 2008). Especially the height of vegetation well below 30 cm seems to be crucial for the selection of foraging areas (Böhm & Pegoraro 2011). This has been confirmed by a few previous studies on habitat use and feeding ecology at the Konrad Lorenz Research Center's Northern Bald Ibis colony (Fritz *et al.* 2007; Kirnbauer 2004; Krejci 2015; Markut 2005). Local enhancement, and hence simple socially transmitted information of the location of food was more important regarding foraging decisions than the characteristics of the substrate (Meran 2002). But the choice of foraging sites was also affected by abundance and composition of food items (Markut 2005).

Because of its conservation status, its highly social structure, and its fission-fusion dynamics, the Northern Bald Ibis was selected as model species. Furthermore, the availability of these birds in Austria at the study sites and the local management (long-term monitoring, individually marked colony with a combination of coloured leg rings) are the main reasons to use the sedentary, free roaming and semi-tame Northern Bald Ibis colony of the Konrad Lorenz Research Center in Grünau im Almtal as a research model in my PhD thesis. This work would not have been possible with the Moroccan population, because in this population not a single individual is individually marked, making individual distinction and distinction between sexes impossible.

The Konrad Lorenz Research Center was the first institution worldwide to successfully establish a sedentary free-ranging Northern Bald Ibis colony from zoo offspring in 1997, which was the first free-living colony north of the Alps in 400 years

(Kotrschal 1999). Ever since, this colony provides an opportunity for collecting long-term data on social behaviour (*e.g.* Sorato & Kotrschal 2006; Tintner & Kotrschal 2002), contributing know-how for different reintroduction and conservation projects in the past (Böhm & Pegoraro 2011). The birds of this colony do not show migratory behaviour, instead they overwinter in the aviary of the Cumberland game park (adjacent to the research center), where they are supplemented with food and provided with freshwater and heating lamps. However, they fly to a neighbouring village (Molln, Upper Austria) each year during summer and return to Grünau im Almtal during autumn. Furthermore, up to 50% of the juveniles in this colony show dispersal behaviour at the end of summer/beginning of autumn, but some of them return at the end of autumn (Böhm *et al.* 2020).

AIMS AND OBJECTIVES OF THE STUDY

My PhD thesis intends to improve the understanding of the link between affiliative behaviour and physiology (i.e. excreted corticosterone metabolites and endoparasite burden) and factors that shape habitat use and site fidelity during the breeding and non-breeding season in the Northern Bald Ibis by applying fundamental research and employing state of the art methodology (i.e. GPS telemetry). The collected data can be used to inform conservation management and support future conservation decisions and strategies to manage extant colonies or reintroduce new colonies. The following topics and questions were addressed:

(1) **Enzyme immunoassay validation.** Which enzyme immunoassay is best-suited for the analysis of excreted immune reactive corticosterone metabolites in the Northern Bald Ibis? **(Chapter I)**

(2) **The role of affiliative behaviour.** Does affiliative behaviour modulate concentrations of excreted immune reactive corticosterone metabolites and endoparasite burden in relation to the reproductive season? **(Chapter I)**

(3) **Factors affecting social networks.** Do season, sex, age and reproductive partners affect social interactions in a colonial breeding bird species? **(Chapter II)**

(4) **Effects of bio-loggers.** Do GPS-transmitters influence behavioural and physiological parameters of an endangered bird species? **(Chapter III)**

(5) **Factors affecting space use and site fidelity.** Do sex, age class, breeding and non-breeding season affect space use and site fidelity patterns in an endangered bird species? **(Chapter IV)**

The reproductive season may elicit stress responses and consequently affect the immune system, which could impair survival and reproductive success (Svensson *et al.* 1998). **Chapter I** addresses the seasonal role of affiliative behaviour (i.e. initiated and received) on concentrations of excreted immune reactive corticosterone metabolites and endoparasite burden (as measured by the number of samples containing endoparasites products) in Northern Bald Ibis in accordance with the social buffering hypothesis, which describes the social buffering effect of conspecifics on the stress response (Cohen & Wills 1985). Affiliative interactions between focal individuals were observed and droppings – used for non-invasive determination of excreted corticosterone metabolite concentrations and endoparasite burden (i.e. nematode eggs and coccidian oocysts) – were collected. I analysed the data in relation to pair bond status (i.e. paired and unpaired individuals) and season (i.e. reproductive and post-reproductive season), and predicted affiliative behaviour, excreted corticosterone metabolite levels, and endoparasite burden to be modulated by those parameters. Specifically, I expected (1) paired individuals to engage more often in affiliative interactions, to have lower excreted corticosterone metabolite levels, and to exhibit lower endoparasite burden compared to unpaired individuals, (2) affiliative interactions to be more frequently observed during the reproductive season than during the post-reproductive season, and (3) higher excreted corticosterone metabolite concentrations and endoparasite burden during the reproductive season.

However, a necessary step in the use of non-invasive methods to measure faecal glucocorticoid metabolites is the validation and selection of the most species-specific appropriate enzyme immunoassay to measure excreted corticosterone metabolites in the respective model species (Sheriff *et al.* 2011; Touma & Palme 2005). In **Chapter I**, I address this issue experimentally: a handling experiment was conducted in order to induce handling stress. Droppings were collected (1) one day prior to the handling experiment to measure excreted baseline corticosterone metabolite levels, and (2) following the stressor over a 6-hour period. Finally, several assays, that work well in a variety of bird species, were compared to select the best-suited one.

Conspecifics may not only buffer the stress response, which is also reflected by a lower endoparasite load, but also facilitate the transmission of parasites or diseases between individuals (Drew & Perkins 2015). Thus, monitoring social relationships and consequently the risk of transmission of parasitic infections can aid wildlife conservation. This is the first study to date to examine social networks in Northern Bald Ibis. However, studies that have used social network analysis as a tool have rarely examined threatened or declining species (Webber & Vander Wal 2019). **Chapter II** is the first study to address social networks in the Northern Bald Ibis and examines the effect of season, age, sex, and reproductive partner on social interactions during autumn and winter. I observed the occurrence of affiliative and agonistic interactions (i.e. initiated and received) between all colony members and recorded inter-individual distances (i.e. proximity), which were analysed using social networks. I predicted (1) seasonal differences in inter-individual distances, (2) higher frequencies of agonistic interactions for males than females, in particular during winter compared to autumn, (3) comparable levels of affiliative interactions in both females and males, and (4) older individuals to occupy more socially central positions within the social network.

Furthermore, to investigate space use patterns and site fidelity in Northern Bald Ibis, I equipped focal individuals with GPS-transmitters. However, to ensure observation of the birds' natural behaviour even while being GPS-tagged, potential effects on their behaviour and physiology need to be considered. **Chapter III** focuses on experimentally testing the effects of GPS transmitters on behaviour (i.e. locomotion, foraging and maintenance behaviour, dorsal feather preening, social interactions) and physiological parameters (i.e. concentrations of excreted corticosterone metabolites). I considered these effects in two different contexts: (1) in captivity focussing on short-term effects and (2) in the field focussing on intermediate-term effects. Focal individuals were randomly allocated to two experimental groups and a control group: (1) logger group (GPS-tagged birds), (2) handling group (birds experienced handling procedure, but were not equipped with a GPS transmitter), and (3) control group (birds neither experienced GPS-tagging nor handling). Behavioural data and droppings to measure excreted corticosterone metabolite concentrations were collected prior to (baseline observations), during and after the tagging/handling procedure. I predicted (1) the strongest effects of GPS transmitters on behaviour shortly after tagging (i.e. increased maintenance behaviour and dorsal feather preening in GPS-tagged birds compared to control birds), but no long-term effects, (2) GPS-tagged birds to exchange fewer affiliative behaviours than control birds, (3) that levels of excreted corticosterone metabolites would be elevated shortly after GPS-tagging and handling, but would then return to baseline.

Synergies between social behaviour, physiology, and movement analyses can allow conclusions to be drawn about the vulnerability of a population, as survival is inextricably linked to patterns of space use (Berger-Tal *et al.* 2011). Furthermore, site fidelity is expected to be favoured in habitats that promote survival and/or reproductive success, which may limit optimal habitat selection and lead to conservative habitat use (Switzer 1993). Little is known about how reproduction and individual traits shape movement patterns and site fidelity of the Northern Bald Ibis. In **Chapter IV**, I used GPS transmitters to understand and predict whether and two what extent individual (i.e. sex, age) and abiotic (i.e. season) factors influence space use patterns and site fidelity (i.e. frequently used locations). Focal individuals were GPS-tagged during 1 to 4 years. I measured (1) the area used, (2) the consistency of space use over time and the consistency of flyways between areas, (3) site fidelity to locations of interest, and (4) factors (sex, age class, biological relevant season) that shape space use and site fidelity patterns. I predicted (1) Northern Bald Ibis to differ in space use size and site fidelity depending on age class and season, but still show an extremely large overlap between individuals, (2) consistent use of specific sites, and (3) that space use and site fidelity would not vary by sex.

BACKGROUND

1. Part I: Physiological implications of social behaviour

Sociality influences survival and reproductive success in group living animals (Ryder *et al.* 2009). For instance, individuals face high costs during the reproductive season in terms of energy/resource allocation, as well as ecological (e.g. predation risk) and behavioural (e.g. territorial defence) factors (Williams 1966; Zera & Harshman 2001). These costs often result in elevated glucocorticoid secretion and impaired immune functions (Sheldon & Verhulst 1996; Vitlic *et al.* 2014), which increases susceptibility to parasitic infections (Eberhardt *et al.* 2013). An individual's stress response can be lowered by the presence of a conspecific, in particular individuals with strong affiliative relationships. This phenomenon is described as the social buffering hypothesis (Cohen & Wills 1985). But, contact with conspecifics may also increase the risk of transmission of parasitic infections and diseases on the one hand (Hirsch *et al.* 2013), and on the other hand, the stability of social relationships may also influence reproductive success (Silk 2007). The study of social relationships (i.e. social network analysis) reveals the causes and consequences of social interactions (Wasserman & Faust 1994) and consequently provides insights into the social dynamics of group-living animals (Croft *et al.* 2011). To date, however, there has been little discussion of the synergy of physiology and social behaviour in Northern Bald Ibis conservation actions, as management has tended to focus on monitoring populations of the species (AEWA 2018), regulating development pressures and growing tourism, conserving traditional agricultural areas, preventing disturbance around breeding sites in Morocco, and translocation and reintroduction projects (Böhm *et al.* 2020).

This section gives a brief overview of (1) the non-invasive measurements of glucocorticoids and the importance of validating the enzyme immune assay used to analyse glucocorticoid metabolites, (2) the effects of prolonged glucocorticoid elevation, (3) the role of affiliative social relationships in stress response, and (4) social relationships in complex social systems (i.e. social networks).

1.1. Non-invasive measurements of glucocorticoids

The hypothalamic-pituitary-adrenocortical (HPA) axis modulates the primary stress-response to a stressor. Briefly, the HPA axis is activated by the release of corticotrophin-releasing factor (CRF) from the hypothalamus, leading to the release of adrenocorticotropic hormone (ACTH) from the anterior pituitary. Glucocorticoids (such as cortisol or corticosterone, which are regarded as 'stress-hormones') are then released by the adrenal cortex (de Kloet *et al.* 2005, 2008; Johnson & Meerveld 2012; Möstl 2014; Figure 3). Corticosterone is the primary avian glucocorticoid released during a physiological stress response (Carsia & Harvey 2000).

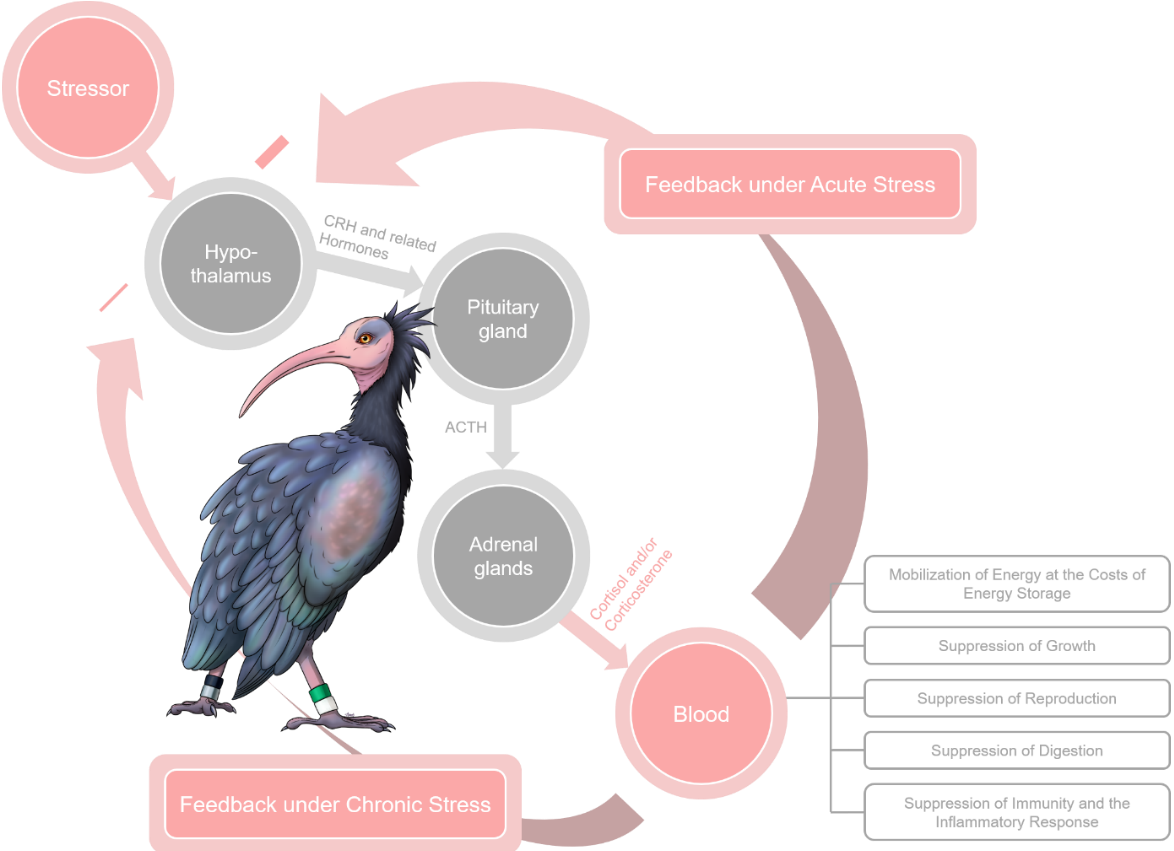

Figure 3. Hypothalamic-pituitary-adrenal (HPA) feedback loop in response to a stressor. Concentrations of glucocorticoids released during physiological stress responses to acute stress return to baseline levels after the exposure to a stressor ends. Chronic stress, however, causes a not efficient working feedback system, which causes long-term and detrimental effects, such as mobilization of energy, suppression of growth, suppression of reproduction, suppression of digestion or suppression of immunity and the inflammatory response. CRH – corticotropin-releasing hormone, ACTH – adrenocorticotropic hormone. Adapted from Boonstra *et al.* (1998), p. 372, accessed 21 January 2021.

In previous years, glucocorticoids were primarily measured via blood sampling; however, this method is frequently not possible when working with wildlife, partly because the procedure of capture, restraint and invasive physiological surveys can have an impact on the measurement itself (Maho *et al.* 1992; Roy & Woolf 2001; Vleck *et al.* 2000). Thus, non-invasive procedures, i.e. measuring faecal glucocorticoids, are more frequently used with wildlife as the expression of natural behaviours in wild animals is not compromised (Ludders *et al.* 2001; Wasser *et al.* 2000). Steroids are metabolised in the liver and their metabolites are excreted, thereby enabling the detection of immune-reactive glucocorticoid metabolite levels in the faeces of mammals or droppings of birds. Faecal concentrations of immune-reactive glucocorticoid metabolites are representative for the circulating levels in the blood (Möstl *et al.* 2005; Palme & Möstl 1997; Touma & Palme 2005).

Measuring excreted glucocorticoid concentrations non-invasively via enzyme-immunoassays measures concentrations of hormone metabolites (metabolic end products of the hormone) but not the actual hormone (a signal molecule in the blood) (Goymann 2012). A careful physiological or biological validation of the immunoassay is needed (Möstl *et al.* 2005; Möstl 2014; Palme *et al.* 2005) for proper interpretation of hormone metabolite data obtained from wildlife (i.e. ensure that the assay used is approriate for the specific species and concentrations are measured accurately). This validation is essential, because faeces contain various substance types in addition to hormone metabolites, which increases the likelihood of cross-reactions to structurallly similar metabolites when glucocorticoid metabolites are measured in contrast to plasma glucocorticoids (i.e. high concentration of the biologically active hormone in the blood; Goymann 2012; Sheriff *et al.* 2011; Touma & Palme 2005).

1.2. Effects of prolonged glucocorticoid elevation

Coping with stressors, such as adverse environmental conditions (e.g. drought, thermal extremes) or social factors (e.g. stability of social relationships, dominance hierarchy), is partly mediated by short-term elevation of glucocorticoid concentrations (Raulo & Dantzer 2018). Individuals infested with parasites are also more likely to show a short-term increase of glucocorticoid concentrations in response to infection rather than prolonged elevated glucocorticoid secretions

(O'Dwyer *et al.* 2020). In addition, stressors could include specific technologies, such as GPS-based technologies, required to answer certain scientific questions. However, tagging animals with GPS transmitters (as discussed in **Chapters 2.1** and **III**) could elicit stress responses that lead to increased glucocorticoid concentrations. To prevent long-term increases in glucocorticoid concentrations and consequent changes in natural behaviour and physiological patterns, the effects of the devices used need to be evaluated.

Prolonged elevated secretion of glucocorticoids can have detrimental effects, such as negative effects on memory and cognitive functions (Finsterwald & Alberini 2014), an increase in oxidative stress (Costantini *et al.* 2011), a reduction in fitness (Breuner *et al.* 2008), or impaired immune system, which increases susceptibility to disease (Dhabhar 2009; Dwyer & Bornett 2004; Eberhardt *et al.* 2013). Stress-induced deficits, such as impaired spatial reference memory, decreased retention of learned performances (Conrad 2010), and biased decision-making process (i.e. bias towards habitual behavioural responses instead of goal-oriented decisions) could impair an individual's survival in a rapidly changing environment (Dias-Ferreira *et al.* 2009). Individuals may face a trade-off when exposed to elevated glucocorticoid secretion favouring survival while inhibiting reproduction (Wingfield 2013). However, previous research findings have been contradictory and suggest the environment to play a major role in the effect of elevated glucocorticoids on fitness (Breuner *et al.* 2008). Furthermore, prolonged elevation of glucocorticoids can also lead to impaired immune system and in turn to a higher intensity of gastrointestinal parasitic infection (Arlet *et al.* 2015; Brown & Fuller 2006; Corlatti *et al.* 2012; Martínez-Mota *et al.* 2017; Romeo *et al.* 2020). Thus, individuals repeatedly exposed or experiencing prolonged exposure to a stressor may be less efficient at defence against parasitic infections and consequently reproductive output. But, parasites can also act as stressors, inducing a release in glucocorticoids (Pedersen & Greives 2008; Pérez *et al.* 2019; Warne *et al.* 2011) and resulting in a cycle, with elevated glucocorticoid levels leading to increased parasite burden which consequently leads to further increase in glucocorticoid levels (Beldomenico & Begon 2010, 2015). The synergistic interaction between physiological stress response and parasitic infection certainly varies with parasite species and also depends on the life stage of the respective parasite (Eberhardt *et al.* 2013; Hammond *et al.* 2019; Lindsay *et al.* 2016; Romeo *et al.* 2020).

1.3. The role of affiliative social relationships in stress response

Strong affiliative social relationships are able to buffer physiological stress responses and thereby benefit immune function and alleviate parasite burden (Hennessy *et al.* 2009; Sachser *et al.* 1998). In which form and with which social partners (i.e. a single companion or within a social unit) social buffering occurs strongly depends on the species' social organisation. For example, social buffering might be absent in solitary species, while group-living animals form intense affiliative relationships throughout their life span (e.g. mother-infant, pair partners; Hennessy *et al.* 2009). Experimentally tested colony-living guinea pigs (*Cavia aperea f. porcellus*) exhibited an attenuated increase of glucocorticoid secretion in relation to novel environment when in the presence of a bonded partner; but, no effect was apparent when tested with a strange individual or one they only shared a weak bond with (Hennessy *et al.* 2006). Similar patterns were found in the Muenster yellow-toothed cavy (*Galea monasteriensis*), a monogamous wild guinea pig species, and the monogamous zebra finch (*Taeniopygia guttata*) when separated from and reunited with their pair partner (Adrian *et al.* 2008; Remage-Healey *et al.* 2003). Buffering of a physiological stress response during social density stress situations in greylag geese (*Anser anser*) can also be attributed to passive social support within large families (Scheiber *et al.* 2005b). Furthermore, social relationships have a positive impact on individual immune system and thereby have strong fitness implications, as shown in carrion crows (*Corvus corone*) with strong social bonds having lower excretion rates of gastrointestinal parasite products (Wascher *et al.* 2019). Even though infection susceptibility could be reduced by having social connections (Balasubramaniam *et al.* 2016), contrasting evidence shows that contact to other conspecifics might also mediate disease transmission (Drew & Perkins 2015). Disease transmission and social relationships between individuals can be tracked using social network analysis.

1.4. Social relationships in complex social systems (i.e. social networks)

Social relationships within a population affect fitness (Pruitt & Riechert 2011; Szipl *et al.* 2019; Turner *et al.* 2020), movement (Spiegel *et al.* 2016), dominance (Bierbach *et al.* 2014; Funkhouser *et al.* 2018), predation (Hasenjager & Dugatkin 2017; Kelley *et al.* 2011), animal personality (López 2020), information transfer (Firth *et al.* 2016) or disease transmission (Emch *et al.* 2012; Hirsch *et al.* 2013). In particular, reproductive success may be influenced by the quality of long-term social relationships (Silk 2007) and by the degree of centrality of the social position within a group (Szipl *et al.* 2019). But, social stability within a group is not only determined by aggressive and affiliative interactions, but also by long-term stability of group structure and dynamics, sexual and social partner relationships, family units, and coalitions (Snijders *et al.* 2017).

Understanding variations in social interactions related to sex, age, season, and reproduction (Bengston & Jandt 2014; Estrada *et al.* 2017) reveals ‘with whom’ and ‘to which extent’ individuals interact within a social group. Seasonal-specific sociality in vultures, for instance, is shaped by ecological factors, age and social attraction (van Overveld *et al.* 2020). Social network analysis provides remarkable insights into complex social structures (Croft *et al.* 2011). Animal social networks represent the observed patterns of associations or interactions and consist of nodes linked with edges. Nodes represent individuals or groups, whereas edges represent the association or interaction between two nodes, indicating the presence or absence of a relationship (Farine & Whitehead 2015). Thus, social network analysis can be used as a tool to study whether group social structures change and which individuals are instigating structural changes (Snijders *et al.* 2017). Dispersal, for instance, strongly depends on how well individuals are embedded in the social structure of a group (Blumstein *et al.* 2009; Farine & Whitehead 2015).

2. Part II: Movement ecology in social animals

Social relationships as well as behavioural traits can be modulated by environmental changes (Pinter-Wollman *et al.* 2009), such as habitat loss and fragmentation (Banks *et al.* 2007), but also by encountering novel environments due to dispersal, migration or relocation (Dufour *et al.* 2011; Norris & Marra 2007; Pinter-Wollman *et al.* 2014) and reintroduction projects (Franks *et al.* 2020). Translocated African elephants (*Loxodonta africana*), for example, seem to benefit from social relationships with conspecifics after arriving at a novel environment; however, these social associations decrease over time, suggesting that with increasing habitat familiarity benefits of social associations diminish (Pinter-Wollman *et al.* 2009). But, social conditions (e.g. intraspecific and interspecific interactions) can also alter habitat selection and space use by using the presence of conspecifics/heterospecifics as an indicator of habitat quality or by increasing distance or association with specific individuals (Fletcher 2007; Garabedian *et al.* 2018; Howery *et al.* 1998; Nocera & Betts 2007). Developing an understanding of how social behaviour affects patterns of space use is important for understanding wildlife habitat relationships, which in turn is necessary for effective conservation (Rotenberry *et al.* 2006). However, little is known about the space use patterns and site fidelity of the Northern Bald Ibis in relation to breeding and individual differences.

This section introduces (1) GPS transmitters as a tool and possible associated effects, (2) space use in free living animals, and (3) site fidelity.

2.1. GPS transmitters as a tool and possible associated effects

Global positioning system (GPS) telemetry technology eases and allows the flexibility to collect wildlife fine-scale spatio-temporal location data even in remote habitats (Cagnacci *et al.* 2010) and on specific research topics that were previously not feasible to implement in some animal species, such as large pelagic fish (e.g. Sims *et al.* 2009), migratory songbirds (e.g. Deppe *et al.* 2015; Hallworth & Marra 2015; Pedersen *et al.* 2019) and long-distance migratory mammals (e.g. Bartlam-Brooks *et al.* 2011; Seidler *et al.* 2015; Wall *et al.* 2013). Over the past few decades, these miniature electronic devices ('bio-loggers') have greatly improved in terms of device miniaturization and advancements in battery life, which aids tracking wildlife (Kays *et al.* 2015).

However, inappropriate use of GPS transmitters could have detrimental effects on the health, behavioural traits and physiology of an individual. The weight of GPS transmitters should not exceed 3% of the body weight of the tagged individual (Phillips *et al.* 2003). For example, GPS-tagged birds appear to have lower flight speeds. This effect seems to be more pronounced the heavier the bird is, depending on the additional weight of the GPS transmitter (Tomotani *et al.* 2019). This would certainly have an impact on wild birds. In addition, the placement of GPS transmitters should be carefully considered as this could have a great impact on individual flight patterns: Northern Gannets (*Sula bassana*) with tail-mounted GPS transmitters had problems with balancing the weight and consequently had higher energy expenditures (Vandenabeele *et al.* 2014). Furthermore, in two populations of Northern Bald Ibis a unilateral corneal opacity was detected, which may be associated with carrying GPS transmitters (Fritz *et al.* 2020). Thus, investigating the effect of GPS transmitters is of crucial importance to study animals under correct ethical and scientific considerations.

Combined with behavioural ecology, GPS-based technology can be used to gain an understanding of an individual’s fitness, as the knowledge of how and why animals move is one element of the mechanistic explanations of animal ecology (Cagnacci *et al.* 2010). GPS transmitters are for example appropriate to investigate the following ecological themes: resource use, behaviour (e.g. foraging behaviour), space use patterns, home range, migration/dispersal, movement ecology or human-wildlife conflict (Latham *et al.* 2015; Figure 4). In my case, GPS transmitters were used to infer about space use patterns and resource use.

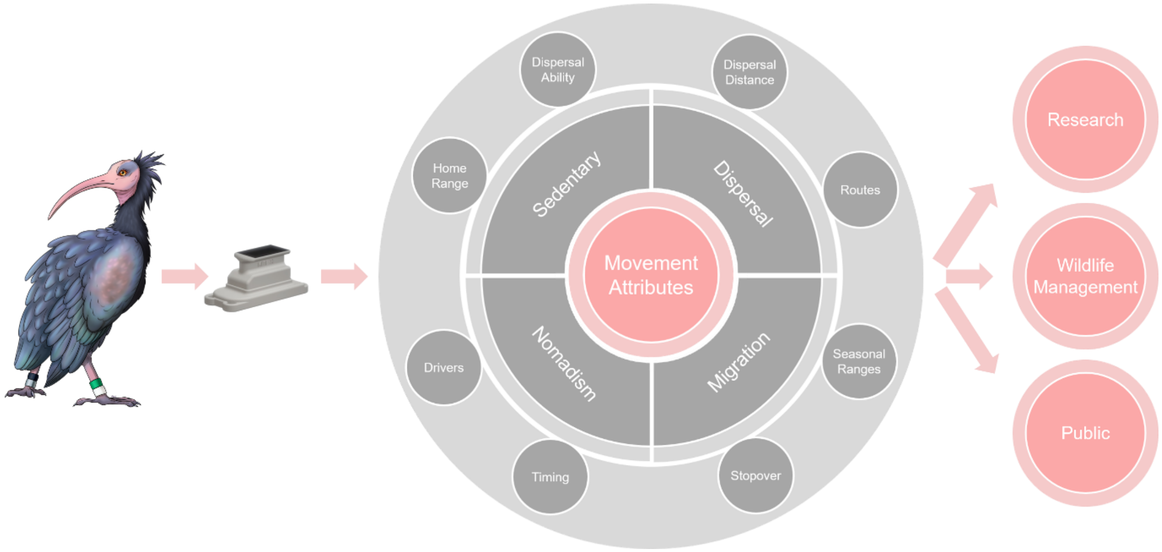

Figure 4. Understanding movement attributes, i.e. migration, dispersal, sedentary and nomadism, of a study population can aid wildlife conservation. It is essential to understand the characteristics of these movement types, such as movement pathways, home range patterns or the timing of movements. The data collected via tracking devices inform research, wildlife management and the public about the vulnerability of a population. Adapted from Allen & Singh (2016), p. 4, and Wall *et al.* (2014), p. 597, accessed 08 March 2021.

2.2. Space use in free living animals

In a broad sense, an 'ecological niche' is more or less species-specific (Hardesty 1975). Within this wider frame, individuals actively create their specific niche by interacting with their environment (Odling-Smee *et al.* 1996). Individual fitness would be optimised by interacting optimally with environmental factors such as food and the social network (Levins 1968), which may change over life history (Gadgil & Bossert 1970). The optimal use of the environment may be constrained by competitors and predators and may depend on the features of the environment itself. For example, a broad niche (occupied by generalists) generally fits well with living in a high environmental stochasticity (highly unpredictable variability; Levins 1968). Nevertheless, ecological factors will affect reproduction and survival (Johnson 2007). For instance, higher survival rates and breeding success were found in black-tailed godwits (*Limosa limosa islandica*) in high-quality summer and winter habitats as compared to individuals selecting poor habitats (Gunnarsson *et al.* 2005).

Home range size is affected by individual traits such as age, sex (Ofstad *et al.* 2019), or reproductive status (Aronsson *et al.* 2016) and abiotic factors such as season (Ofstad *et al.* 2019). Reintroduced brown bears (*Ursus arctos*) in the Italian Alps, for example, had more expansive home ranges during the mating season compared to spring or autumn and location-based data informed about settlement decisions, which leads to a better understanding of the rapid population decline (Preatoni *et al.* 2005). Furthermore, GPS-based research informs whether ongoing management investment is warranted, as was highlighted by high territorial fidelity and consistent use of territories in a threatened population of hooded plovers (*Thinornis rubricollis*; Weston *et al.* 2009).

2.3. Site fidelity

Individuals often return to specific areas within their home range, such as foraging areas or water holes. Site fidelity is a common form of behavioural consistency animals may develop in habitats supporting survival and/or reproductive success (Piper 2011; Switzer 1993). Advantages may include: (1) knowing the location of food, (2) efficient movement, (3) effective escape from predators, and (4) reduced conflict with neighbours (Piper 2011). Hence, site fidelity may be adaptive under certain conditions, but also constrains optimal and flexible choice of habitat.

Habitat variability (Switzer 1993) and habitat quality (Switzer 1997), as well as age (Pyle *et al.* 2001; Switzer 1997), sex (Beheler *et al.* 2003) or breeding success (Shields 1984), have been identified as major contributing factors in developing site fidelity. Organisms may be site-faithful to sub-optimal habitats when the costs of searching for an optimal one (e.g. possible injuries, predation risk, familiarity with a new territory) are greater than the costs of returning to the sub-optimal one. Thus, developing site fidelity may be advantageous in relatively predictable habitats, for example, with respect to predator avoidance (Switzer 1993). However, philopatry (synonymous to site fidelity) could also be driven by constraints, such as neophobia, limited exploration potentials (Mettke-Hofmann *et al.* 2002) and learning abilities (McCall & Kelly 2002) or high social cohesion (e.g. dilution to limit predation risk; Hamilton 1971). All these factors would favour conservative habitat use.

PART I

Physiological implications of social behaviour

CHAPTER I

RESEARCH ARTICLE

Seasonal differences of corticosterone metabolite concentrations and parasite burden in northern bald ibis (Geronticus eremita): The role of affiliative interactions

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Picture credit: Verena Pühringer-Sturmayr

Abstract

The reproductive season is energetically costly as revealed by elevated glucocorticoid concentrations, constrained immune functions and an increased risk of infections. Social allies and affiliative interactions may buffer physiological stress responses and thereby alleviate associated effects. In the present study, we investigated the seasonal differences of immune reactive corticosterone metabolite concentrations, endoparasite burden (nematode eggs and coccidian oocysts) and affiliative interactions in northern bald ibis (*Geronticus eremita*), a critically endangered bird. In total, 43 individually marked focal animals from a free-ranging colony were investigated. The analyses included a description of initiated and received affiliative interactions, pair bond status as well as seasonal patterns of hormone and endoparasite levels. During the reproductive season, droppings contained parasite eggs more often and corticosterone metabolite levels were higher as compared to the period after reproduction. The excretion rate of endoparasite products was lower in paired individuals than in unpaired ones, but paired animals exhibited higher corticosterone metabolite concentrations than unpaired individuals. Furthermore, paired individuals initiated affiliative behaviour more frequently than unpaired ones. This suggests that the reproductive season influences the excretion patterns of endoparasite products and corticosterone metabolites and that affiliative interactions between pair partners may positively affect endoparasite burden during periods of elevated glucocorticoid levels. Being embedded in a pair bond may have a positive impact on individual immune system and parasite resistance.

Introduction

The reproductive season is considered socially and energetically costly when compared to the post-reproductive one (Svensson *et al.* 1998; Williams 1966). Such costs of reproduction are often manifested by up-regulated glucocorticoid secretion and constrained immune functions (Hanssen *et al.* 2005; Sheldon & Verhulst 1996). For instance, territorial male Alpine chamois (*Rupicapra rupicapra*) showed elevated cortisol metabolite concentrations and parasite levels during the mating season as compared to the post-mating period (Corlatti *et al.* 2012). Chronically elevated glucocorticoid levels suppress immune function (Vitlic *et al.* 2014) and the down-regulation of the immune system may increase the susceptibility to parasitic infections (Brown & Fuller 2006; Dhabhar 2009; Dwyer & Bornett 2004; Eberhardt *et al.* 2013). The physiological costs of parasitic infection can be confirmed by experimentally removing parasites. Wild mice populations (*Peromyscus maniculatus* and *P. leucopus;* Pedersen & Greives 2008) and cliff swallows (*Petrochelidon pyrrhonota;* Raouf *et al.* 2006) showed reduced corticosterone levels when intestinal nematodes or hematophagous ectoparasites were removed. Furthermore, in greylag geese (*Anser anser*) parasite excretion decreased throughout the parental season, which has been suggested to be related to the high energetic costs of the reproductive season (Wascher *et al.* 2012). Furthermore, in altricial birds parental care is modulated by the offspring's parasite load (Avilés *et al.* 2009; Tripet & Richner 1997). When caring for parasitized offspring, blue tit parents (*Parus caeruleus*) increased their feeding rates in compensation (Tripet & Richner 1997), whereas reduced parental effort was shown in male spotless starlings (*Sturnus unicolor*) with parasitized nests (Avilés *et al.* 2009). However, information on the contribution of other individual life-history traits (e.g. sex, age, social status) is difficult to obtain in free-living social animals, which may complicate the analyses of parasite infection patterns (Papazahariadou *et al.* 2008; Wascher *et al.* 2012).

Social allies and affiliative behaviour may help buffering physiological stress responses (Frigerio *et al.* 2003; Kikusui *et al.* 2006; Sachser *et al.* 1998; Scheiber *et al.* 2005b; Stöwe *et al.* 2008). For example, Barbary macaques (*Macaca sylvanus*; Young *et al.* 2014) and wild chimpanzees (*Pan troglodytes schweinfurthii*;

Wittig *et al.* 2016) showed decreased glucocorticoids in the company of a bonding partner, suggesting that affiliative interactions may provide a buffer against stressors, benefitting immune function and alleviating parasite burden. Furthermore, in chicks of domestic hens *(Gallus gallus domesticus*), the presence of the mother buffered the stress response to an aversive stimulus (Edgar *et al.* 2015) and in greylag geese the presence of socially supportive family members reduced corticosterone secretion (Frigerio *et al.* 2003; Scheiber *et al.* 2005b; Wascher *et al.* 2012). Although individual levels of corticosterone metabolites in parental geese were negatively correlated with the number of offspring (Scheiber *et al.* 2005b), the excretion of nematode eggs increased with family size (Wascher *et al.* 2012), indicating that parental effort is costly (Kotrschal *et al.* 1998). A recent study in northern bald ibis (*Geronticus eremita*) showed that paired individuals excreting high levels of endoparasite products during the reproductive season also engaged in more allopreening behaviour (Frigerio *et al.* 2016).

We presently aim at investigating the seasonal differences of concentrations of excreted immune reactive corticosterone metabolites (CM), parasite burden (as measured by the number of samples containing endoparasite products) and frequencies of affiliative behaviour between the reproductive and post-reproductive season in the free-roaming and individually marked colony of northern bald ibis at the Konrad Lorenz Research Station (Austria). This seasonally monogamous and year-round colonial species breeds in dense colonies and forages in flocks, that often split into subgroups of different sizes (Böhm & Pegoraro 2011). Pair bond stability changes with time in seasonally monogamous species, with strong social bonds among the adults at the start of each reproductive season and loose ones during the post-reproductive period (Rowley & Bateson 1985). Especially for paired individuals we expected higher levels of corticosterone metabolites and endoparasite products in the reproductive period as compared to the post-reproductive one. We also expected paired individuals to engage more often in affiliative interactions than unpaired ones, with interactions occurring more frequently during the reproductive season than outside.

We distinguished between initiated and received affiliative behaviour since they may differ in their effects on glucocorticoid secretion, as measured by a reduced excretion of CM (Shutt *et al.* 2007), self-directed behaviours (selfgrooming/self-scratching; Fraser *et al.* 2008; Radford 2012) or heart rate (Aureli *et al.* 1999; Feh & de Mazières 1993; Sato & Tarumizu 1993). We predicted that receiving rather than initiating affiliative behaviour may lead to a greater reduction of glucocorticoid levels and hence to reduced parasite burden.

Material and methods

This study complies with all current Austrian laws and regulations concerning the work with wildlife. Catching, restraining of the birds, observing the animals and collecting droppings were performed under Animal Experiment Licence Number 66.006/0026-WF/V/3b/2014 by the Austrian Federal Ministry for Science and Research (EU Standard, equivalent to the Animal Ethics Board). We confirm that the owner of the land, the Duke of Cumberland, gave permission to conduct the study on this site. All data were collected non-invasively. Birds were habituated to the presence of humans.

Field site and study animals

The study was conducted in Grünau im Almtal (Upper Austria, 47°48'E, 13°56'N). The free-ranging colony of northern bald ibis was established in 1997 at the Konrad Lorenz Research Station (KLF) in Grünau im Almtal by hand-raising zoo-bred chicks (Tuckova *et al.* 1998) in coordination with the European Breeding Programme (EEP; Böhm 1999). Since 2001 the birds raise their chicks autonomously and the colony has grown to more than 40 individuals. The animals are housed in a large aviary, which is open year round, at the local Herzog-von-Cumberland game park. They are free-flying and roam the foraging grounds in the Almtal-region, returning to the aviary for roosting at night and for breeding. From November to May the birds are supplied twice a day with hash made from 1-day-old chicks mixed with soaked dog food (Alpha Multicroc, RWA Raiffeisen Ware Austria AG, Vienna, Austria). All birds are individually marked with a combination of coloured leg rings. At the start of data collection, the colony consisted of 43 birds (focal animals; $N_{males}=24$, $N_{females}=19$). The age ranged from 0 to 16 years (mean: 4.2). According to the classification described by Böhm & Pegoraro (2011) focal individuals were assigned to three different age classes: (1) juvenile (first year after hatching, N=6), (2) sub-adult (second and third year after hatching, N=15) and (3) adult (from fourth year on, N=22). Details about focal individuals (name, sex, year of hatching, pair bond status) are given in S1 Table.

Data collection

Behavioural data and individual droppings were collected over a period of 112 days between 15 May 2015 and 31 October 2015. Days of data collection were irregularly distributed over the sampling period, as the northern bald ibis population flew to Molln (Upper Austria, 47°53'E, 14°15'N; 25 km linear distance from Grünau im Almtal; 112 days in Grünau and 76 days in Molln) and stayed there from August until October. In Molln, standardised data collection was not possible, due to inaccessible foraging grounds (e.g. cow paddocks). Hence, data collected in Molln were excluded from the analyses. We included both the reproductive and post-reproductive season in this study. The reproductive season was determined as the time from rearing to fledging of the offspring (generally from May to mid-June, provisioning phase), whereas the post-reproductive season lasted from mid-June to October. Due to individual variations in the start of egg-laying, beginning and end of both periods were determined separately for each breeding pair depending on the hatching date of the offspring.

Behavioural data. The behaviour was measured by applying a continuous recording method (Altmann 1974; Martin & Bateson 2007) for each focal individual. All focal observations were evenly distributed during daylight hours (i.e. between 08.00 AM and 08.00 PM) to avoid temporal biases. Behavioural protocols lasted 5 minutes per individual and were recorded using the software CyberTracker (CyberTracker Conservation, Cape Town, South Africa; www.cybertracker.org; Pimm *et al.* 2015). The frequencies of affiliative behaviours initiated and received by the focal birds, such as greeting, preening, preening invitation, mutual bill shaking and contact sitting were monitored in the aviary or the nearby foraging grounds (for a detailed description of northern bald ibis' ethogram: see Pegoraro (1992)). In sum, a total of 284 behavioural protocols were collected over the entire period ($\overline{x}$ ± SE: 6.6 ± 0.8 focal observations per individual). The mean frequencies per minute per individual per week were: initiated – 0.72 ± 0.10, received – 0.10 ± 0.04.

Collection of droppings and analysis of corticosterone metabolites. Droppings of the focal individuals were collected in order to determine the amount of (1) CM and (2) excreted endoparasite products (nematode eggs and coccidian oocysts).

Steroid metabolites in droppings represent an integrated, proportional record of the unbound portion of plasma steroids depending on the frequency of defecation and gut passage time (Palme & Möstl 1997). We assumed the gut passage time of northern bald ibises to be 2-3 hours, comparable to the white ibis (*Eudocimus albus)* which are similar in size and diet (Adams *et al.* 2009). The sample collection was performed daily independently of behavioural observations. To account for possible endogenous diurnal variations, droppings were collected during the same time period (04.00 PM to 07.00 PM CET). The samples were collected immediately after defecation in Eppendorf® microtubes (Eppendorf®, Hamburg, Germany), with one sample per tube in order to avoid contamination with other droppings. Due to constraints of dropping collection in the field, the sample size varies in the different analyses. The samples were (1) stored on ice during collection and then frozen at -20 °C within 3 hours after collection for the determination of CM or (2) stored at +6 °C and analysed within 7 days after collection for parasite burden. A total number of 142 droppings were collected for CM analysis (on average: $\overline{x} \pm SE = 3.74 \pm 0.47$ samples per individual) and 130 for parasite burden (on average: $\overline{x} \pm SE = 4.06 \pm 0.57$ samples per individual). The different sample sizes result from the fact that CM and parasite samples were collected independently from each other. CM were determined using an enzyme immunoassay (EIA, selection for the best suited assay see below; Möstl *et al.* 2002) at the laboratory of the Department of Behavioural Biology, University of Vienna (Austria). The intra- and interassay coefficients of variation were below 5%.

Selection of the best-suited assay. Besides the data collection described above, we compared several available enzyme immunoassays in order to select the best-suited one for measuring corticosterone secretion in the northern bald ibis, a necessary step when using such non-invasive methods for measuring faecal glucocorticoid metabolites (Sheriff *et al.* 2011; Touma & Palme 2005).

To evaluate which of the currently available EIAs is best suited for measuring adrenocortical activity of the northern bald ibis, a handling experiment was run on two experimental days in December 2015 and January 2016. Four individuals (2 males and 2 females, S1 Table) were subjected to a handling stress. For baseline CM levels droppings were collected one day prior to the experiment during the same time period in which an increase in CM concentrations was expected in response to the handling stress on the following day (10.00 AM to 12.00 AM). We tested males and females separately on two different days. The focal individuals were captured between 09.30 AM and 09.45 AM on both experimental days to avoid the early morning peaks of adrenocortical activity (Carere *et al.* 2003) and to prevent unnecessary disturbance of the other colony individuals. Upon capture, each bird was put into a cloth bag (approximately 40x45x2 cm) for 10 minutes. Afterwards, the individuals were released into a test room, which was divided into two compartments by a mesh. Both birds were in visual and acoustic contact with each other and with the other members of the colony in the main aviary. We kept the birds to be tested separated from the other birds to prevent cross-contamination of droppings and to enable the simultaneous data collection of two individuals. The test room was enriched with branches and the floor was covered with a clear tarp to facilitate the collection of each dropping. Dropping collection was conducted for 6 hours after the beginning of the experiments (i.e. approximately between 10.00 AM and 04.00 PM). The exact time of defecation was recorded for each sample. An aliquot (0.5 g) of each dropping was extracted with 5 ml 60% methanol (Palme *et al.* 2013). The analysis was run at the Department of Biomedical Sciences, Unit of Physiology, Pathophysiology and Experimental Endocrinology, University of Veterinary Medicine in Vienna (Austria). The following 5 assays, which work well in diverse bird species, were tested on northern bald ibis droppings to determine the best-suited one: a corticosterone EIA (Palme & Möstl 1997; this assay has previously been used for northern bald ibis droppings by Sorato & Kotrschal 2006), an 11-oxoaetiocholanolone EIA (Möstl *et al.* 2002), a cortisone EIA (Stöwe *et al.* 2013), an 11ß-hydroxyaetiocholanolone EIA (Frigerio *et al.* 2004) and a 5α-pregnane-3ß,11ß,21-triol-20-one EIA (Touma *et al.* 2003). All extracts were diluted with assay buffer (1:10) and 50 µl were used for the EIA. All samples were analysed in duplicates. The 11-oxoaetiocholanolone assay (‘best assay’) turned out to be the most appropriate for northern bald ibis droppings, meaning that this assay is considerably more sensitive compared to the others. In fact, it detected higher peak values within the same sample (highest increase of median CM concentration from baseline – best assay: 348 %, corticosterone EIA: 293 %; Fig 1). Furthermore, the ‘best assay’ also detected peaks of CM concentrations over a longer time period after the stress-induced handling, whereas the corticosterone EIA only detected the first peak concentration.

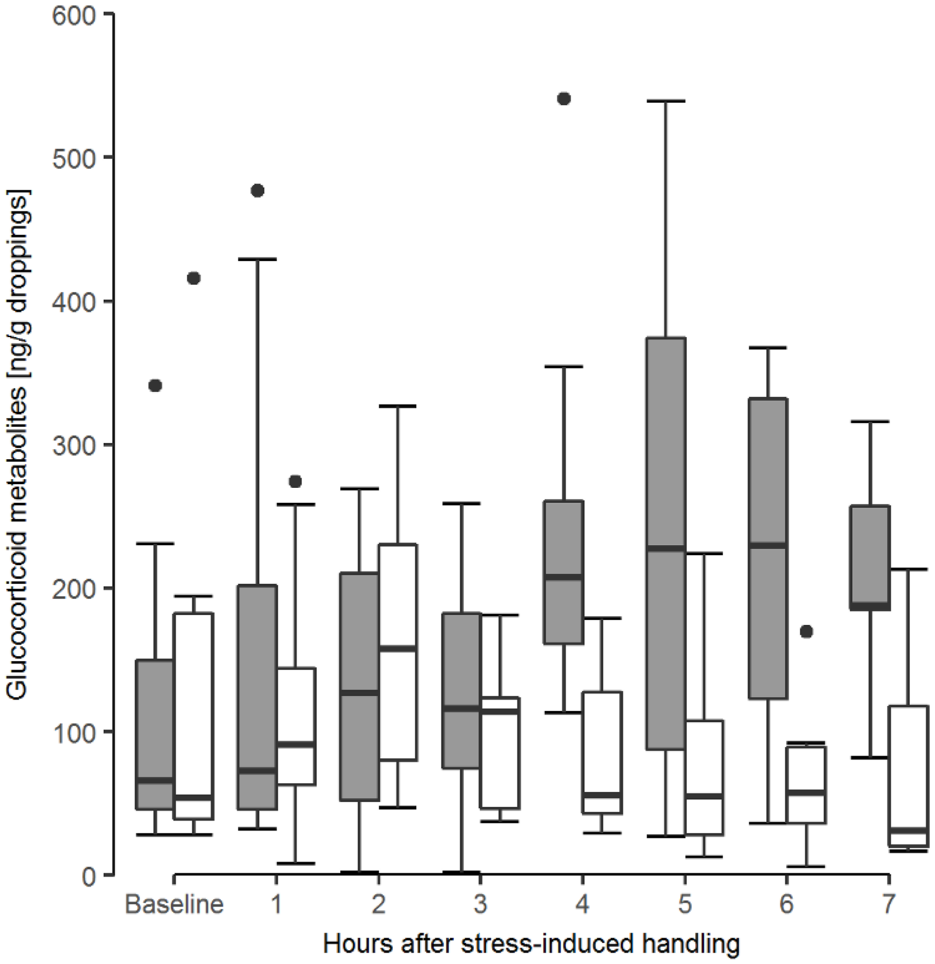

Fig 1. Detected corticosterone metabolite concentrations for two assays. Median (± SE) levels of excreted corticosterone metabolites of all four individuals for the 11-oxoaetiocholanolone enzyme immunoassay (best-suited assay, grey boxplots) and the corticosterone enzyme immunoassay (white boxplots). $N_{individuals}$=4, $N_{samples}$=81.

Parasitological examination. The examination for excreted parasite products (nematode eggs and coccidian oocysts) was done using a flotation method in a McMaster counting chamber (Hiepe *et al.* 1981). At least 0.1 g dropping was diluted with the triple volume of saturated NaCl solution (350 g NaCl, 1000 ml distilled water) and filtered through a sieve to remove large food particles and debris. The remaining solution was transferred into both McMaster counting chambers, in which the excreted coccidian oocysts and nematode eggs were counted. A value for oocysts/eggs per gramme faeces was calculated according to (Hiepe *et al.* 1981):

$$eggs/oocysts\ per\ gramme = \frac{number\ of\ counted\ eggs * volume\ of\ salt\ solution\ (ml)}{volume\ of\ counting\ chambers\ (0.30\ ml) * weight\ of\ dropping\ (g)}$$

Due to generally low parasite egg and oocyst abundance in the samples (percentage of samples containing nematode eggs: 22.52 %; percentage of samples containing coccidian oocysts: 15.32 %), we treated samples either as containing or not containing nematode eggs or coccidian oocysts.

Statistical analyses

All statistical analyses were conducted using R version 3.2.5 (R Core Team 2017) and the additional packages ‘glmmADMB’ (Fournier *et al.* 2012; Skaug *et al.* 2016) for calculation of generalised linear mixed models (GLMM) and ‘MuMIn’ (Barton 2020) for information-theoretic model selection as well as model averaging based on the information criteria. A ratio per minute was calculated for all behavioural parameters observed. Due to few occurrences of behavioural interactions, we treated initiated and received affiliative behaviour as a binomial variable, i.e. occurred or not occurred events, which were taken into further statistical analyses.

To assess which factors influence (1) parasite burden (samples containing nematode eggs and coccidian oocysts – yes/no), (2) initiated (yes/no) and (3) received (yes/no) affiliative behaviour (all three response variables) we used GLMMs with binomial error distribution and logit link function. To analyse which factors influence (4) CM (response variable) we used a GLMM with gamma error distribution and inverse link function. Fixed factors in these models were (1) sex, (2) age, (3) pair bond status (paired, unpaired) and (4) season (reproductive and post-reproductive season). Since the northern bald ibis is a social, seasonally monogamous and colonial species, affiliative interactions can be observed between all colony members. Therefore, we also included pair bond status as a fixed factor in the affiliative behaviour models. Subject identities were included as random factors in all GLMMs to control for between-subject variation and unbalanced design. Field constraints did not allow a regular data collection for the three data sets (parasite burden, CM, affiliative behaviour). Interactions between fixed factors were not considered in the statistical analyses as they did not improve the model fit.

To select the best models, we used an information theoretic approach and calculated all possible candidate models (Burnham & Anderson 2002). We ranked them according to their AICc values (second-order form of Akaike's information criterion to account for small sample sizes; Hurvich & Tsai 1989) and selected the models with ΔAICc ≤ 2 with respect to the top-ranked model. The models were averaged in order to create model-averaged coefficients following (Burnham & Anderson 2002).

Results

Model-averaged results identified season as the strongest determinant of the excretion patterns of nematode eggs and coccidian oocysts. The number of droppings containing endoparasite products was highest during the reproductive season as compared to the time after reproduction (Fig 2). While season was the second-most important variable for corticosterone metabolite (CM) concentrations, it was the least important parameter for initiated affiliative behaviour. During the reproductive season, we found higher CM levels as compared to the post-reproductive period. Affiliative interactions were initiated more frequently during the reproductive season, while the rates decreased in the post-reproductive period (Fig 3).

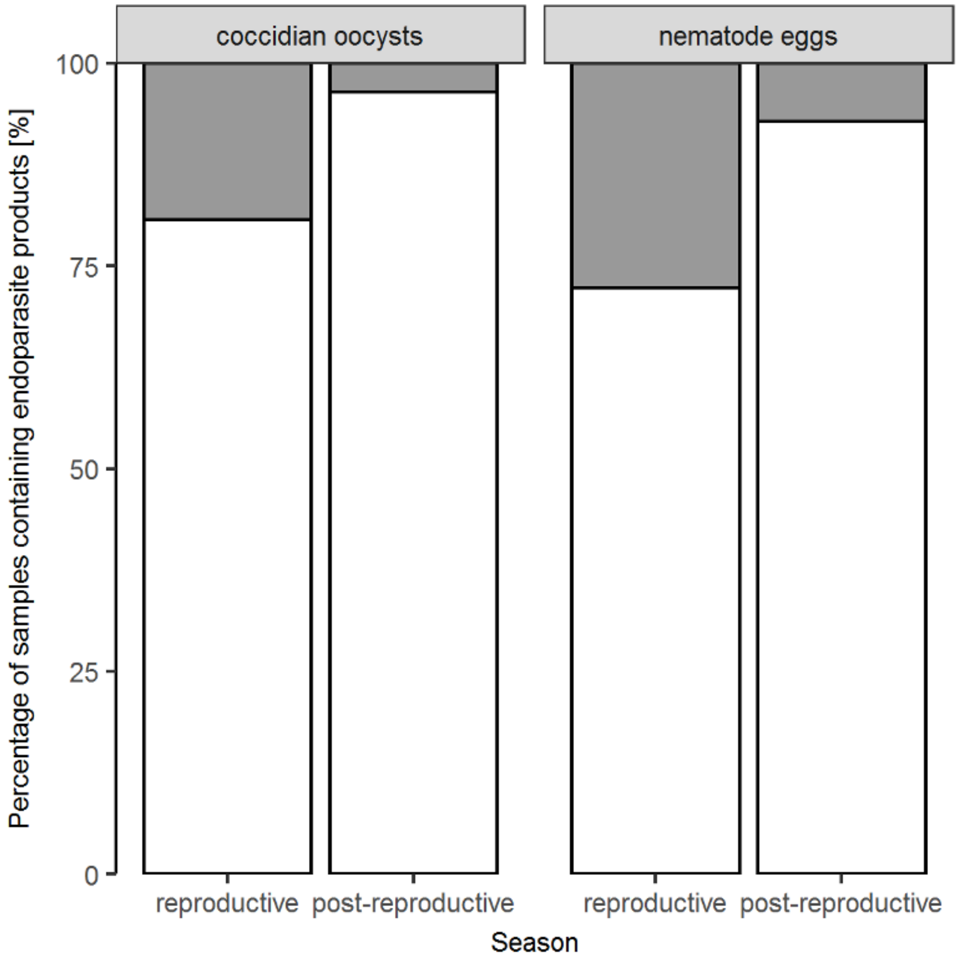

Fig 2. Seasonal differences in excretion patterns of endoparasite products. Percentage of samples containing (grey bars) as well as not containing (white bars) endoparasite products for the reproductive and post-reproductive season. $N_{reproductive}$=83, $N_{post\text{-}reproductive}$=28, $N_{samples}$=111.

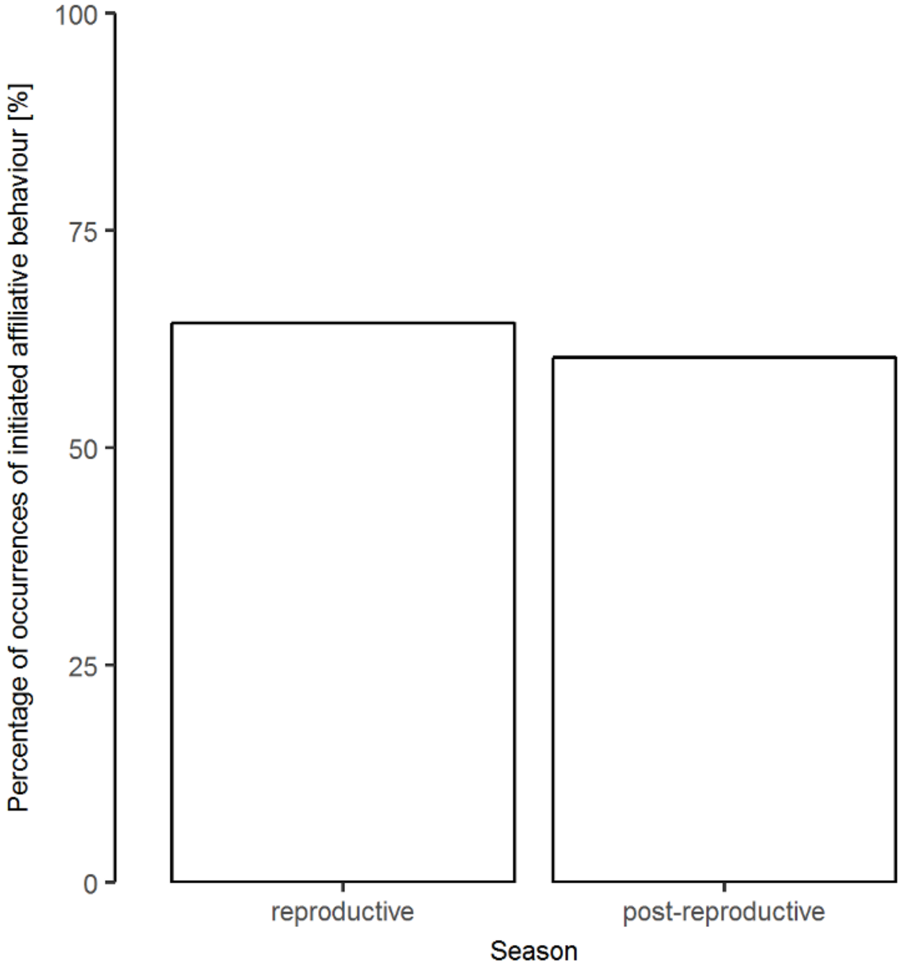

Fig 3. Seasonal differences in engaging in affiliative interactions. Percentage of occurrences of initiated affiliative behaviour for the reproductive and post-reproductive season. $N_{reproductive}$=87, $N_{post-reproductive}$=197.

Pair bond status was the second-most important variable influencing the excretion of coccidian oocysts. Furthermore, pair bond status was indicated as the third-most important variable for nematode egg excretion, CM levels and initiated affiliative behaviour. Paired individuals excreted fewer droppings containing endoparasites (Fig 4) and exhibited generally higher CM concentrations and initiated more often affiliative behaviour as compared to unpaired ones.

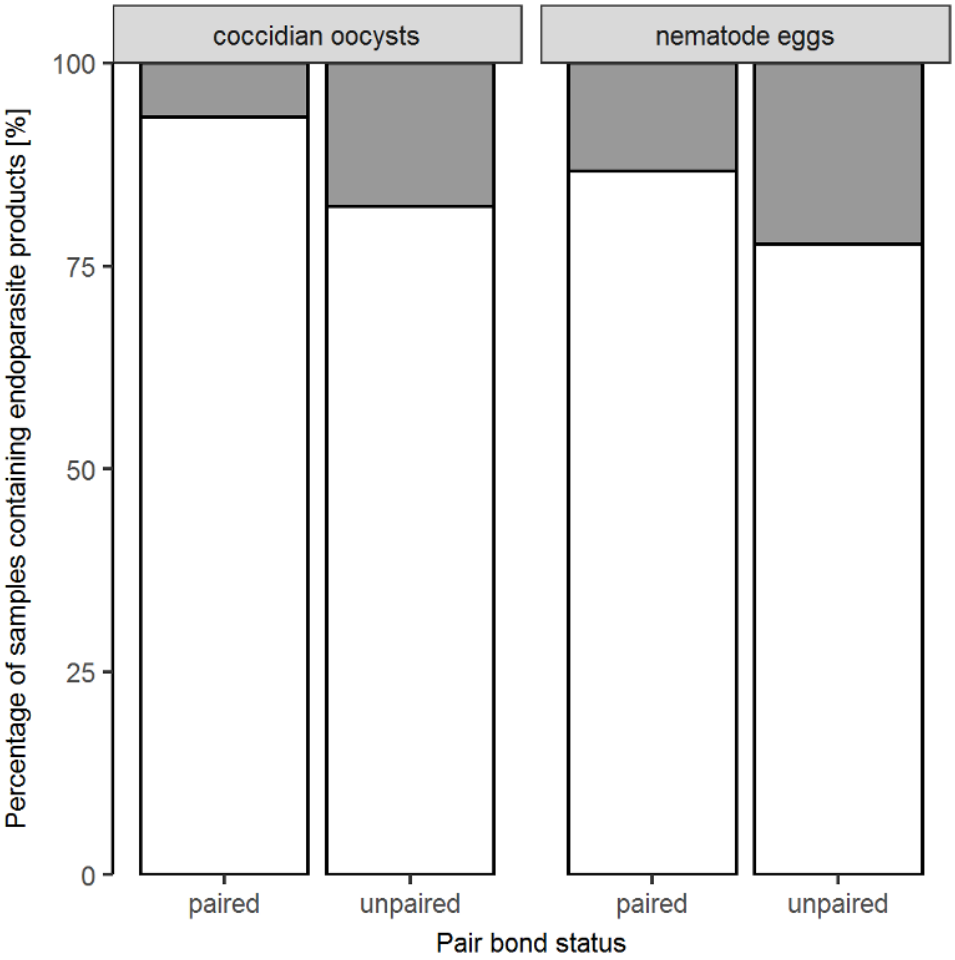

Fig 4. Differences in excretion patterns of endoparasite products depending on pair bond status. Percentage of samples containing (grey bars) as well as not containing (white bars) endoparasite products for paired and unpaired individuals. N_{paired}=10, $N_{unpaired}$=22, $N_{samples}$=130.

We found that initiated affiliative behaviour and the excretion pattern of nematode eggs were best explained by sex. Males initiated affiliative interactions more frequently and excreted a higher number of droppings containing endoparasite products than females. The relative importance indicated the variable sex to be less important for coccidian oocysts. Furthermore, sex had no influence on CM.

The most influential variable on the excretion patterns of CM was age, with juveniles exhibiting higher CM levels compared to adults, whereas sub-adult individuals showed lower concentrations than adults. Furthermore, it was the second-most influential variable for initiated affiliative behaviour. A higher frequency of initiating affiliative behaviour was found in juveniles compared to adults, whereas sub-adults initiated less than adults. Age had the least importance when considering the excretion patterns of coccidian oocysts, with lower excretion rates in juvenile and sub-adult individuals as compared to adult ones. Age, however, did not predict the excretion rate of nematode eggs.

All candidate models with received affiliative behaviour as response variable did not improve penalised model fit over the null model, as assessed by AICc, indicating that variation in the data cannot be explained by any of these factors (Burnham and Anderson 2002).

Statistical details of the top-ranked models are presented in Table 1 and 2.

Discussion

We found different modulation patterns of excreted immune reactive corticosterone metabolites (CM) and endoparasites in the reproductive season as compared to the post-reproductive period in the seasonally monogamous but year-round social northern bald ibis. The reproductive season is energetically costly in terms of egg-laying, incubation and rearing of the offspring (Romero 2002), which was indicated by high CM concentrations during the reproductive period and decreasing CM afterwards. This was mirrored by the decrease of the excretion of endoparasite products as well. In contrast, initiating affiliative behaviour was only weakly modulated by season.

As our data are correlative, we can only speculate about a potential causality between elevated CM concentrations and endoparasite burden. We suggest that the increased excretion of endoparasite products as well as high corticosterone metabolite concentrations during the reproductive season may be the result of a trade-off between reproductive effort and immune function (Sheldon & Verhulst 1996). High CM levels may suppress immune responses (Klein 2000), impairing the defence against parasites. This would explain the similar excretion patterns of endoparasite products and CM during the reproductive and post-reproductive season. Alternatively, we cannot exclude that patterns of endoparasite burden may have also been driven by the phenology of the parasites themselves, meaning that the seasonality of the parasites and their underlying dissemination could result in certain patterns in parasite product excretion, independent of the animals' immune response (Demarais *et al.* 1987; Pap *et al.* 2015; Wascher *et al.* 2012). However,

Table 1. Top-ranked models. Given are the predictors influencing the response variables nematode eggs, coccidian oocysts and initiated affiliative behaviour.

Explanatory variables of each model	Df	logLik	∆AICc	weight
nematode eggs				
season, sex	4	-55.779	0.00	0.712
season, sex, pair bond status	5	-55.599	1.81	0.288
coccidian oocysts				
season, pair bond status, sex	5	-47.226	0.00	0.188
season, pair bond status	4	-48.454	0.29	0.163
season, sex	4	-48.501	0.38	0.155
pair bond status, sex	4	-48.599	0.58	0.141
sex	3	-49.973	1.20	0.103
season, pair bond status, age	6	-46.850	1.45	0.091
season	3	-50.204	1.66	0.082
pair bond status, age	5	-48.110	1.77	0.078
corticosterone metabolites				
age	5	-704.961	0.00	0.513
age, season	6	-704.466	1.19	0.282
age, pair bond status	6	-704.784	1.83	0.205
initiated affiliative behaviour				
sex	3	-285.876	0.00	0.179
sex, age	5	-183.842	0.06	0.174
sex, pair bond status	4	-184.959	0.22	0.160
age	4	-185.083	0.47	0.142
sex, age, season	6	-183.666	1.80	0.073
sex, season	4	-185.794	1.89	0.070
sex, age, pair bond status	6	-183.742	1.95	0.068
age, season	5	-184.787	1.95	0.068
sex, pair bond status, season	5	-184.803	1.98	0.067

Df – degrees of freedom; logLik – log-likelihood; ∆AICc – differences of the second order Akaike information criterion between the best model and the other top-ranked models; weight – Akaike weight.

Table 2. Model-averaged coefficients. Given are the coefficients with adjusted standard errors, lower and upper confidence intervals and relative importance of the top-ranked models.

Parameter (*levels*)	Estimate	Adjusted SE	CI lower limit (2.5 %)	CI upper limit (97.5 %)	Relative importance
nematode eggs					
Intercept	-4.71	1.29	-7.23	-2.18	
season (*reproductive period*)	1.65	0.80	0.07	3.22	1.00
sex (*male*)	2.01	1.12	-0.18	4.20	1.00
pair bond status (*unpaired*)	0.11	0.39	-0.86	1.65	0.29
coccidian oocysts					
Intercept	-3.84	1.22	-6.23	-1.44	
season (*reproductive period*)	0.85	0.88	0.32	2.83	0.68
pair bond status (*unpaired*)	0.75	0.78	-0.22	2.50	0.66
sex (*male*)	0.94	1.14	-0.52	3.72	0.59
age (*juvenile*)	-2.66	2067.99	-9976.96	9945.44	0.17
age (*sub-adult*)	-0.26	0.73	-3.69	0.66	0.17
corticosterone metabolites					
Intercept	4.24	0.19	3.87	4.60	
age (*juvenile*)	0.25	0.43	-0.60	1.10	1.00
age (*sub-adult*)	-0.66	0.29	-1.24	-0.09	1.00
season (*reproductive period*)	-0.04	0.10	-0.42	0.14	0.28
pair bond status (*unpaired*)	-0.04	0.16	-0.80	0.43	0.21
initiated affiliative behaviour					
Intercept	0.31	0.27	-0.22	0.84	
sex (*male*)	0.46	0.35	0.01	1.15	0.79
age (*juvenile*)	0.25	0.55	-0.87	1.83	0.52
age (*sub-adult*)	-0.35	0.42	-1.36	0.03	0.52
pair bond status (*unpaired*)	-0.09	0.21	-0.88	0.27	0.29
season (*reproductive period*)	0.04	0.16	-0.38	0.70	0.28

SE – standard error; CI – confidence interval.

as parasitic infections are often associated with a suppressed immune system (Brown & Fuller 2006; Dhabhar 2009; Dwyer & Bornett 2004) and CM showed similar secretion patterns, parasite phenology alone is probably insufficient to explain the observed patterns.

We further found that males produced more endoparasite-positive droppings than females, suggesting that particularly the male immune system was affected by social investment. This is also indicated by the fact that males in general, independently of age, initiated more affiliative interactions compared to females, which would be expected to function as social support buffering females glucocorticoid secretion. As males are the donors of social support, which benefits the females, they also may generally be more susceptible to infections with parasites due to reduced immune functions as compared to females (Klein 2000, 2004). Another possible explanation for these sex-specific differences may be the immunosuppressive effects of testosterone (Trigunaite *et al.* 2015), whereas oestrogens are thought to enhance immune function (Zuk & McKean 1996). However, Sorato & Kotrschal (2006) showed that excreted testosterone metabolite levels are similar between male and female northern bald ibis, indicating that testosterone alone may not be the major driving factor in parasite infection. Hence, patterns of parasite burden may be influenced by several factors, such as pair bond status, reproductive state and rearing condition (Zuk *et al.* 1998) as well as individual factors such as sex and age (Zuk & McKean 1996) and they may be seen as a result of the interaction of all the factors mentioned above (Wascher *et al.* 2012).

Higher CM levels and excretions of endoparasite products were found in adults compared to sub-adult individuals and adults also initiated more affiliative interactions. This may be linked to sexual maturity and hence to the necessary behavioural and physiological investment into reproduction. As glucocorticoids are the major hormones regulating metabolism (Vegiopoulos & Herzig 2007), this investment is reflected by a greater glucocorticoid up-regulation during the reproductive season as compared to the post-reproductive period (Breuner & Orchinik 2001; Deviche *et al.* 2000; Romero 2002). In contrast, juvenile individuals exhibited higher CM concentrations while having a lower parasite burden than adults and initiated more frequently affiliative interactions. A possible explanation for these age differences may be that age causes changes in the hypothalamic-pituitary-adrenal axis (Chahal & Drake 2007). For instance, plasma corticosterone concentrations in response to a stressor decreased with age in Florida scrub-jays (*Aphelocoma coerulescens*), while the oldest individuals exhibited again greater corticosterone levels (Wilcoxen *et al.* 2011).

Probably due to relaxed pair bond relationships outside the reproductive season in the northern bald ibis (Böhm & Pegoraro 2011), affiliative interactions generally occurred more frequently during the reproductive as compared to the post-reproductive season. Affiliative interactions during the post-reproductive season may be seen as social investment towards old or new pair partners before the start of the new breeding season (Böhm & Pegoraro 2011). As paired individuals exhibited lower excretion patterns of coccidian oocysts compared to unpaired ones, which may indicate that pair partners, via mutual social support, can control endoparasite burden in stressful periods, such as the reproductive season.

Contrary to expectations, we found no link between receiving affiliative behaviour and the excretion of CM and endoparasite products. However, the excretion patterns of endoparasite products were still lower in paired than unpaired individuals. This may indicate that initiating affiliative interactions with social partners may up-regulate immune functions, even though high CM levels are still present. In fact, pair bonded northern bald ibis excreted higher concentrations of CM compared to unpaired ones. Moreover, long-term monogamous avian species, such as greylag geese, show decreased excretion of CM when family members are present during stressful situations (Scheiber *et al.* 2005b, 2009). In separated zebra finch pairs (*Taeniopygia guttata*) for example, elevated corticosterone concentrations returned to baseline levels after reunion with the pair partner (Remage-Healey *et al.* 2003). This implies that familiar individuals are more effective for social buffering than unfamiliar ones (Kiyokawa *et al.* 2014; Rukstalis & French 2005; Wittig *et al.* 2016). Similarly in mammals, male Wistar rats (*Rattus norvegicus*) did not show fear-related behaviours, such as freezing, when smelling the odour of a familiar conspecific (Kiyokawa *et al.* 2014) and squirrel monkey (*Saimiri sciureus*) females showed decreased basal cortisol levels in the presence of a female pair partner (Saltzman *et al.* 1991).

On the other hand, it might be expected that interacting with parasitized conspecifics increase the risk of infection (Martinez-Padilla *et al.* 2012). However, paired individuals were less parasitized with coccidian oocysts than unpaired ones. Furthermore, as being paired is also related to age and dominance (Hepp 1989; Komers & Dhindsa 1989), dominant individuals could defend better resting places, which are less contaminated with faeces.

A previous study on northern bald ibis showed that more nematode eggs were excreted in females than in males during the reproductive season (Frigerio *et al.* 2016), whereas in the present study it was the other way round. Contrary to this previous study, we did not include the egg-laying phase in the data collection, which may be the reason for not finding an elevated excretion of endoparasite products in females. This suggests that the high energetic costs of egg-laying suppress female immune responses in a socially stressful situation. A possible explanation may be that resources are allocated to reproduction during the egg-laying period and hence down-regulate female immune functions (Nordling *et al.* 1998), which may lead to an increase in parasite burden.

We conclude that excretion patterns of endoparasite products and CM concentrations differ in the colonial and seasonally monogamous northern bald ibis according to season. Even though reproduction is energetically costly and may be accompanied by elevated glucocorticoid concentrations (Svensson *et al.* 1998; Williams 1966), affiliative interactions may buffer endoparasite burden during stressful periods. This suggests that being well embedded in a pair bond may have a positive impact on individual parasite burden and therefore also on the immune system, at least for females.

Acknowledgments

We gratefully acknowledge Josef Hemetsberger for helping with catching the birds, Marlon Millard for carrying out the comparison of assays, Elisabeth Pschernig for analysing the droppings, Julia Krejci and Claudia Bär for field assistance.

Supporting information

S1 Table. List of all focal individuals. Name, sex (m=male, f=female), year of hatching, age class, pair bond status as well as involvement in the assay comparison are indicated.

S1 Dataset. Initiated and received affiliative behaviour for single individuals in the reproductive and post-reproductive season.
(csv file)

S2 Dataset. Corticosterone metabolite (CM) concentrations for single individuals in the reproductive and post-reproductive season.
(csv file)

S3 Dataset. Excretion patterns of endoparasite products (coccidian oocysts and nematode eggs) for single individuals in the reproductive and post-reproductive season.
(csv file)

Supporting information

Table S1. List of all focal individuals. Name, sex (m=male, f=female), year of hatching, age class, pair bond status as well as involvement in the assay comparison are indicated.

Name	Sex	Year of hatching	Age class	Breeder	Assay comparison
Othello	m	1999	adult	yes	X
Hera	m	1999	adult	no	
Hombre	m	2002	adult	yes	X
Abraxas	m	2002	adult	no	
Aleppo	f	2006	adult	yes	X
Simon	m	2006	adult	yes	
Loki	f	2006	adult	yes	
Shannara	m	2007	adult	yes	
Cian	m	2008	adult	no	
Schreckse	f	2008	adult	yes	X
North Face	m	2009	adult	no	
Sequoia	f	2009	adult	yes	
Hilda	m	2009	adult	no	
Heidi	m	2010	adult	no	
Rob	m	2010	adult	no	
Balu	m	2010	adult	yes	
Paco	m	2010	adult	no	
Ozzy	m	2010	adult	no	
Tiffi	m	2011	adult	no	
Lukas	m	2012	adult	no	
Hermine	f	2012	adult	yes	
Kurt	m	2012	adult	no	
Kleopatra	f	2013	sub-adult	no	
Khan	m	2013	sub-adult	no	
Elvis	m	2013	sub-adult	no	
Minerva	f	2013	sub-adult	no	
Oniichan	m	2014	sub-adult	no	
Luzifer	m	2014	sub-adult	no	
Luna	f	2014	sub-adult	no	
Chicco	f	2014	sub-adult	no	
Diablo	f	2014	sub-adult	no	
Kira	f	2014	sub-adult	no	
Mocha	f	2014	sub-adult	no	

Quinto	f	2014	sub-adult	no
Sino	f	2014	sub-adult	no
Taska	f	2014	sub-adult	no
Woody	f	2014	sub-adult	no
Aurelia	f	2015	juvenile	no
Azzurro	m	2015	juvenile	no
Sandro	f	2015	juvenile	no
Saphira	f	2015	juvenile	no
Simba	m	2015	juvenile	no
Smirne	m	2015	juvenile	no

CHAPTER II

RESEARCH ARTICLE

Social interactions change with season and age in Northern Bald Ibis

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Picture credit: Roobert Bayer

Abstract

Understanding the association between an individual's position within a social network and its sex and age across seasons can be useful information for conservation management. For example, identifying the social position of females within a group can provide insights into reproductive potential, while the position of juveniles may be related to survival and hence recruitment potential. In the present study, we used social network analysis to investigate the effects of season, sex, age and reproductive partner on social interactions in the endangered Northern Bald Ibis (*Geronticus eremita*). Via focal sampling we recorded the social behaviour of 39 individually marked, free-flying birds for 4 months over two seasons (autumn, winter). We observed the occurrence of affiliative and agonistic interactions and estimated proximity between colony members. We found that (1) individuals were in proximity with more colony members in winter than in autumn, and affiliative interactions occurred more often in winter, (2) older individuals occupied more central positions in the proximity network irrespective of sex, (3) males engaged more than females in agonistic interactions, whereas females received more affiliative interactions than males irrespective of age, and (4) most affiliative interactions occurred between former or potentially prospective reproductive partners. Our findings suggest that social relationships could modulate inter-individual distance and there may be sex-related differences in the investment into pair bond maintenance. Overall the findings of sex- and age-related differences in behaviour and social position contribute to understanding factors associated with breeding success and mortality risk in an endangered bird species.

Keywords: affiliative interactions, agonistic interactions, juvenile recruitment, colonial, *Geronticus eremita*, proximity, social network, conservation, endangered species

Introduction

Sociality influences survival and reproductive success (Davies *et al.* 2012) via modulating the costs and benefits associated with predation risk, access to food (Krause & Ruxton 2002), and information (Dall *et al.* 2005). Trade-offs between foraging behaviour and antipredator behaviour are well-documented (Verdolin 2006), and the strength of association has been shown to be modulated by social factors (e.g., group size, group composition), individual factors (e.g., age, sex), and environment (e.g., habitat structure, season; Boucherie *et al.* 2016; Lehmann *et al.* 2007; Strandburg-Peshkin *et al.* 2017; Widdig *et al.* 2001). Affiliative interactions, for instance, can be used to quantify social relationships in complex social systems (Wey *et al.* 2008). Intense social relationships are observed between reproductive partners as well as parents and offspring (Dunbar & Shultz 2010), but also between unrelated group members (Boucherie *et al.* 2016; Cameron *et al.* 2009; Lehmann *et al.* 2007; Palagi & Cordoni 2009; Silk *et al.* 2006).

Understanding behavioural variation associated with sex and age in relation to group-level attributes is particularly important for conservation management (Bengston & Jandt 2014; Estrada *et al.* 2017). Reproductive success may be influenced by the quality of long-term social bonds (Silk 2007) as well as by an individual's social position within a group. Highly social female White-Faced Capuchin Monkeys (*Cebus capucinus imitator*) with many affiliative ties, for example, occupy a central social position and have increased offspring survival as compared to other females in the same group (Kalbitzer *et al.* 2017). Mortality risk may also be associated with an individual's social position within a group (Kurvers *et al.* 2014). Yellow-Bellied Marmots (*Marmota flaviventris*) with few affiliative ties, for instance, tend to experience high mortality risk (Blumstein *et al.* 2009). In contrast, agonistic networks can generate information about the competitive abilities of individuals. Older adult Yellow-Bellied Marmots seem to initiate more and receive fewer agonistic interactions than younger adults (Wey & Blumstein 2010). This may increase male reproductive success, because females tend to prefer competitive males (Hirsch & Maldonado 2011). Affiliative interactions are shaped by socio-positive relationships (Hirsch *et al.* 2012), while inter-individual distance (i.e., proximity) within a group is shaped by agonistic interactions and food competition

(Hirsch *et al.* 2012) as well as predator avoidance (Romey & Wallace 2007). Social relationships within groups can be quantified by network analysis, which is a useful tool to quantify sex and age patterns of affiliative and agonistic interactions and proximity in group living animals. Such knowledge can be applied to better understand individual variation in species of conservation concern (Jacoby *et al.* 2012; Snijders *et al.* 2017).

An individual's decision about 'with whom' and 'to which extent' to interact in a group can be affected by intrinsic (e.g., motivation, sex, age) and extrinsic (e.g., proximity, group composition) factors that may vary across seasons (Whirligig Beetles (Coleoptera, Gyrinidae): Romey & Wallace 2007; Yellow-Bellied Marmots: Wey & Blumstein 2010; White-Faced Capuchins: Crofoot *et al.* 2011). For instance, in complex social systems, where individuals tend to associate with friends of their friends, such long-term social relationships are known to modulate the number of affiliative ties among members of a group (Vervet Monkeys (*Chlorocebus pygerythrus*)*:* Borgeaud *et al.* 2016; Spotted Hyenas (*Crocuta Crocuta*)*:* Ilany *et al.* 2015). Relationship patterns may dynamically change across time as individuals join or leave a group (Blonder *et al.* 2012; Kubitza *et al.* 2015) in the course of seasonal migratory and dispersal processes (Blumstein *et al.* 2009; Idani 1991; Pinter-Wollman *et al.* 2009) as well as reproductive phases (Brent *et al.* 2013; Hamede *et al.* 2009).

Understanding the social network of threatened group-living animals is a core challenge for behavioural ecologists especially when the group composition is seasonal. In this study, we explore patterns of social behaviour and inter-individual distance (i.e., proximity) in the Northern Bald Ibis (*Geronticus eremita*), an endangered (BirdLife International 2020) colonial breeding species with fission–fusion foraging patterns. In addition to changes in seasonal movement, such as dispersal and/or local migration, and the formation of seasonally monogamous reproductive pairs, diurnal patterns of association form as the group roosts together at night and forages in subgroups during the day (Böhm & Pegoraro 2011). Individuals tend to form new reproductive pairs each year, though in some cases, partners of the previous year re-pair (Böhm & Pegoraro 2011; Wickler *et al.* 1985). The species is colonial throughout the year (del Hojo *et al.* 1992). Eggs are generally laid between March and May (del Hojo *et al.* 1992). Juveniles are cared for by the parents until approximately 2 weeks after fledging (Böhm & Pegoraro 2011). A social dominance hierarchy is generally established between the members of a colony, in which dominance rank increases with age (Sorato & Kotrschal 2006) and males are dominant over females (Böhm & Pegoraro 2011). Younger birds are more likely to disperse than older birds (Böhm *et al.* 2020). Juveniles seem to have a different overwintering area than adults, which was observed in the extinct Middle East population (Lindsell *et al.* 2009). In this seasonally and socially dynamic system, understanding how age, sex and reproductive partners affect patterns of relationship between individuals can contribute to our knowledge of the potential link between sociality and fitness. Northern Bald Ibis affiliative interactions between pair partners scaled negatively with endoparasite burden during periods of elevated stress (e.g., reproductive period; Puehringer-Sturmayr *et al.* 2018) suggesting that being embedded in a pair bond may have a positive impact on individual fitness (Frigerio *et al.* 2016). Therefore, Northern Bald Ibis might be a suitable model to investigate the relationships between an individual's network position (including other metrics, such as density) and risks (e.g., disease transmission, increased competition) and opportunities (e.g., access to social information) with respect to reproduction and survival.

In the present study, we assessed the effect of season (autumn and winter), sex, age and reproductive partner on proximity between individuals and social behaviour (i.e., affiliative and agonistic interactions between colony members) in a free-flying and individually marked colony of Northern Bald Ibis. We tested the following predictions: (1) there will be an effect of season on inter-bird proximity and the number of agonistic and affiliative interactions, as Northern Bald Ibis engage in pre-breeding displays during autumn and establish new pair bonds during winter (Böhm & Pegoraro 2011), (2) there will be an effect of sex, age and reproductive partner on the observed patterns. Specifically, we predict (1) more agonistic interactions in males during winter than in autumn in competition for mates and nest sites, (2) therefore, generally more agonistic interactions in males than females, and (3) comparable levels of affiliative behaviours in males and females due to relatively symmetrical patterns of interaction within pairs (Sorato & Kotrschal 2006). We also predict that older and more experienced birds will occupy more socially central positions (determined through both affiliative and agonistic interactions in separate social networks) within the group during both seasons associated with known benefits of socially central positions for survivorship in males and females (Archie *et al.* 2014; Kalbitzer *et al.* 2017; Stanton & Mann 2012). Older and experienced birds may profit from a socially central position by reducing stress load via affiliative ties (Puehringer-Sturmayr *et al.* 2018), by increasing fitness via the engagement in breeding activities (Formica *et al.* 2012; Kalbitzer *et al.* 2017), and by gaining access to resources via agonistic encounters and rank acquisition (Kulahci *et al.* 2016).

Methods

Study population and area

A colony of free-flying Northern Bald Ibis was established at the Konrad Lorenz Research Center (KLF) in 1997 in coordination with the European Breeding Programme (Böhm 1999; Tuckova *et al.* 1998). This research facility is situated 5 km south of Grünau im Almtal/Upper Austria (47.852778°N, 13.955556°E). The birds are housed in a year-round open aviary (approximately 20 × 15 × 7 m [L × B × H]; referred to as ‘nesting site’ hereafter) in the local Cumberland Game Park. The aviary is used for roosting as well as for breeding in spring. The birds can leave the aviary at any time and roam the foraging grounds in the area. During winter (from mid-December until March) and depending on the harsh alpine weather conditions, the ibis generally stay at their nesting site. The birds are supplemented with food twice per day during winter periods when resources are scarce and later during spring at the continuation of the breeding season (hash made from 1-day-old chicks and beef heart, mixed with insects and water-soaked dog food; generally from November to May). All the birds are individually marked with coloured leg rings. Birds were habituated to the presence of humans. Observations were conducted in the surroundings of the Konrad Lorenz Research Center (i.e., meadows and a river with gravel banks) and the adjacent Cumberland Game Park (i.e., at their nesting site). At the start of data collection, the colony consisted of 39 individuals (24 males and 15 females, aged from 7 months to 17 years; mean age ± SD = 3.92 ± 4.52; Table S1).

Data collection

Data were collected from 21 October 2016 until 28 February 2017. The observation period was divided into two phases: (1) autumn, data collected from October to December and (2) winter, data collected from January to February. Observations were performed between 0800 AM and 0400 PM of all birds present at that time. We did focal observations of all birds by applying a continuous recording method (Altmann 1974) with each protocol lasting 10 min. Each individual was observed 46.5 ± 1.7 times (mean ± SE), totalling 1814 observation protocols. TS collected a total number of 890 protocols during autumn ($N_{\text{protocols field}} = 727$, $N_{\text{protocols aviary}} = 163$) and a total number of 924 protocols during winter ($N_{\text{protocols field}} = 211$, $N_{\text{protocols aviary}} = 713$). All behavioural data were collected with the software Prim8 Mobile (mobile computing to record nature, https://www.prim8software.com/; McDonald & Johnson 2014). We monitored frequencies of initiated and received affiliative (greeting, bill shaking, clasped necks, preening invitation, preening, contact sitting) and agonistic behaviours (threat, threat greeting, pecking, defensive threat, displacement, attempted displacement, fighting; for a detailed description of the listed behaviours see Pegoraro 1992). Additionally, proximity (< 0.5 m, based on previous observations; measured as duration) of the focal animal to other colony members was measured by visual estimation. For each colony member that came within a 0.5 m radius of the focal individual during the 10 min observation time, we recorded the duration of the proximity between the focal bird and other colony members. Proximity estimation for ibis was trained before starting data collection by estimating and then measuring the distance between bins.

Data analysis

Social network analyses and calculation of network metrics were performed in Ucinet v. 6.699 (Bogatti *et al.* 2002). The randomization procedures to determine if the networks are 'non-random' were computed in R version 4.0.2 (R Core Team 2020). For the visualisation of the networks, we used the software Gephi 0.9.2 (Bastian *et al.* 2009). To analyse the influence of age on the position of the individuals within the network, the age in months was calculated for each focal animal. Since preliminary analysis showed differences in the network metrics (i.e., degree, in-degree, out-degree, eigenvector centrality) of proximity and affiliative interactions between autumn and winter (Wilcoxon signed rank test with continuity correction conducted via R version 3.6.1 (R Core Team 2019; see results), we analysed the two seasons for all response variables in separate models.

Proximity (i.e., all colony members within 0.5 m of the focal individual) was measured to analyse the inter-individual distance during natural foraging and roosting. Four directed and two undirected social networks were created (Farine & Whitehead 2015) for affiliative and agonistic interactions (one directed network each for autumn and winter) as well as proximity (one undirected network each for autumn and winter) split by season. Nodes were defined as the individuals within the colony and edges represented the interactions between those individuals. For affiliative and agonistic networks, edges represented the raw frequency count of interactions between individuals. In the proximity network, a simple ratio index (time observed together/time both observed * 100) was used to calculate the edge weights. Social networks were examined at node-, dyadic- and network-level. To measure individual variation in sociality at the node-level, we calculated different network metrics for each individual in each network representing initiated and received social interactions, i.e., weighted degree (sum of all individuals that interacted with a specific individual), weighted in-degree (corresponds to received affiliative and agonistic behaviours; number of colony members from whom an interaction is received), weighted out-degree (corresponds to initiated affiliative and agonistic behaviours; number of colony members towards which an interaction is initiated) and eigenvector centrality (a measure of social centrality within the network which is proportional to the sum of the centralities of an individual's neighbours). Those network metrics were selected, because we distinguished between initiated and received behaviours, and because in Northern Bald Ibis, affiliative interactions increase during the pre-breeding and breeding season and decrease after the offspring fledged; also, most affiliative interactions occur between former and prospective mates. Degree and eigenvector centrality measure the number of incident links and the quality of those links (i.e., the importance of nodes in a network), which is an important measure to assess how an individual's associations differ between sex of the interactants and change with season and age.

Binary networks (connection between two individuals was coded as 1 and no connection between two individuals was coded as 0) were used to calculate density at the network-level (proportion of possible connections used within a network).

To assess whether associations among pairs of individuals deviated from random variation, we performed pre-network randomizations using data stream permutations for focal sampling data collection protocols and compared the strength of associations of the original and permuted data sets via t-test with the Animal Network Toolkit Software (ANTs) R package (Sosa *et al.* 2020). Data stream permutations swap a single association in each permutation and this permutation can be controlled according to the focal observation number.

Due to the non-independence of network data and consequently the violation of the assumptions of classical statistical analyses, we applied a random permutation approach. Using Node-Level Regression with 1000 permutations, we investigated which factors influenced social structure in the Northern Bald Ibis. Node-Level Regression performs a basic Ordinary Least Squares (OLS) linear regression and uses random permutations method for constructing sampling distributions of R-squared and slope coefficients to estimate standard errors and significance (Hanneman & Riddle 2005). We defined (1) degree (i.e., proximity), (2) out-degree (i.e., initiated affiliative and agonistic behaviours), (3) in-degree (i.e., received affiliative and agonistic behaviours) and (4) eigenvector centrality (i.e., proximity, initiated and received affiliative and agonistic behaviours) as dependent variables. Sex and age (in months) were included as independent variables.

At the dyadic-level a Double Dekker Semi-Partialling Multiple Regression Quadratic Assignment Procedure (MRQAP; Dekker *et al.* 2007) with 1000 permutations was used to examine whether same sex, differences in age and reproductive partners predict proximity and social interactions (affiliative and agonistic interactions) between individuals. MRQAP performs a regression between a dependent matrix (i.e., observed data) and one or more independent matrices (e.g., similarities in attributes of nodes such as sex). The double semi-partialling algorithm proceeds in two steps: (1) a standard multiple regression is computed across corresponding cells of the dependent and independent matrices and (2) together rows and columns of the matrices are randomly permuted, after which the regression is recomputed. To estimate standard errors, this step is repeated

1000 times. For each coefficient, the proportion of random permutations that showed a coefficient as extreme as the one for observed values is counted. We conducted six separate MRQAPs with the network proximity in autumn, proximity in winter, agonistic interactions in autumn, agonistic interactions in winter, affiliative interactions in autumn and affiliative interactions in winter as the dependent matrices, while sex-based homophily (same sex), age-based heterophily (differences in age in months) and reproductive partners (i.e., previous ones before 2017 and partners in 2017) were used as the independent matrices. For the homophily matrix, same sex dyads were coded as 1, while different sex dyads were coded as 0. In the heterophily matrix, the absolute difference of age in months between dyads was calculated. Former or prospective reproductive partners were coded as 1 and other conspecifics as 0.

Results are presented as mean + standard deviation.

Results

Proximity patterns

The proximity network strength of association deviated from random variation during autumn (t_{observed} = 32.687, $t_{\text{permutation mean}}$ = 36.389, $p_{\text{one-tailed}}$ = 0.032) and winter (t_{observed} = 29.470, $t_{\text{permutation mean}}$ = 35.765, $p_{\text{one-tailed}}$ = <0.001). We found an effect of season, reproductive partner and age on proximity patterns, but no differences in sex. In autumn, individuals spent less time in close proximity (i.e., <0.5 m) to conspecifics than in winter. The social centrality position of individuals within the colony did not differ between seasons (Table S2).

Autumn

Network density was high (97.3%), meaning that almost all individuals within the colony were generally in close proximity to each other. Individuals spent more time in close proximity to previous or new reproductive partners compared to other colony members. Sex-based homophily or age-based heterophily did not influence proximity patterns within the colony (Table S3). No sex differences were found in proximity patterns and centrality position (Figure 1a; weighted $\text{degree}_{\text{males}}$ = 34.88 + 13.29, weighted $\text{degree}_{\text{females}}$ = 32.47 + 12.83, eigenvector $\text{centrality}_{\text{males}}$ = 0.15 +

0.07, eigenvector centralty$_{females}$ = 0.14 + 0.07). However, older individuals spent generally more time in close proximity to other colony members and thus occupied a more central position within the network than younger individuals (Table S4).

Winter

Network density decreased during winter (84.4%) as compared to autumn, meaning that all individuals were generally less often in close proximity to each other compared to autumn. Colony members spent more time in close proximity to previous or new reproductive partners compared to other individuals. Sex-based homophily and age-based heterophily had no effect on proximity patterns (Table S3). Sex did not influence proximity patterns and centrality position within the network (Figure 1b; weighted degree$_{males}$ = 63.92 + 15.08, weighted degree$_{females}$ = 56.00 + 18.97, eigenvector centrality$_{males}$ = 0.15 + 0.06, eigenvector centrality$_{females}$ = 0.14 + 0.08). Older birds spent more time in close proximity to other colony members and occupied more central positions (Table S4).

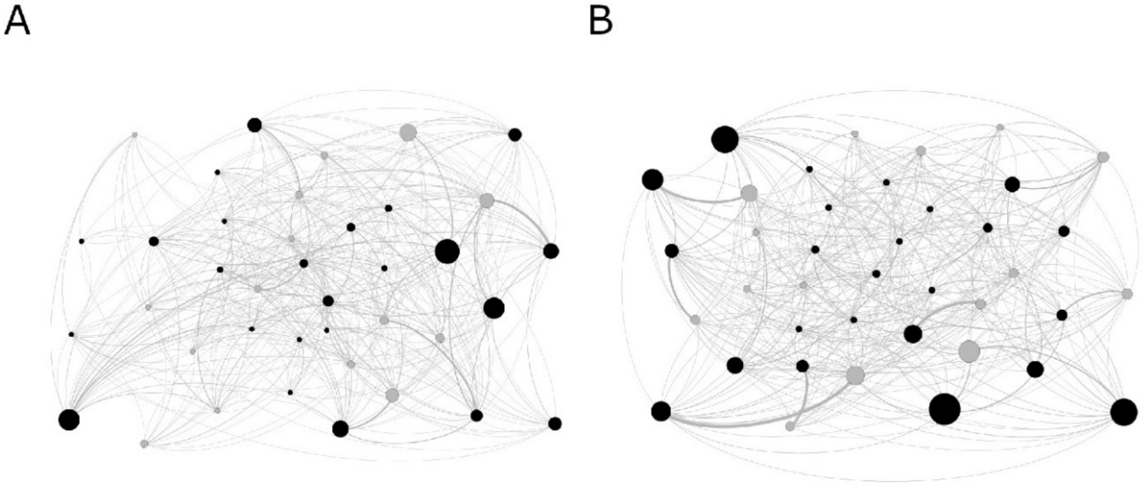

Figure 1. Undirected proximity networks of the Northern Bald Ibis colony during autumn (a) and winter (b). Males are highlighted in black, females in grey. Node size increases with the age of the individuals. Edge size represents how often an individual was observed near another colony member. N$_{males}$ = 24, N$_{females}$ = 15

Agonistic interactions

The agonistic association network deviated from random variation during autumn (t_{observed} = 9.245, $t_{\text{permutation mean}}$ = 24.900, $p_{\text{one-tailed}}$ = 0.006) and winter (t_{observed} = 9.655, $t_{\text{permutation mean}}$ = 23.384, $p_{\text{one-tailed}}$ = <0.001). We found no effect of season or reproductive partner, but effects of age and sex on patterns of agonistic interactions. Initiated and received agonistic interactions as well as the centrality position within the network did not differ between autumn and winter (Table S2).

Autumn

A network density of 18.4% indicated low numbers of possible connections within the agonistic network during autumn. Agonistic behaviours were not shown towards previous or new reproductive partners. Sex-based homophily had no influence on the selection of interaction partner (Table S3) and sex did not modify initiating or receiving agonistic interactions (Figure 2a; out-$\text{degree}_{\text{males}}$ = 10.63 + 8.57, out-$\text{degree}_{\text{females}}$ = 8.87 + 7.29, in-$\text{degree}_{\text{males}}$ = 8.46 + 5.23, in-$\text{degree}_{\text{females}}$ = 12.33 + 4.56). The centrality positions occupied within the social network did not vary with sex or age (Table S4; eigenvector $\text{centrality}_{\text{males}}$ = 0.14 + 0.06, eigenvector $\text{centrality}_{\text{females}}$ = 0.16 + 0.08). Agonistic interactions occurred mostly between individuals of similar age (Table S3). Younger individuals received more and initiated fewer agonistic interactions (Table S4).

Winter

As in autumn, the network density of the agonistic network during winter was 18.4%, indicating only few connections between conspecifics. Previous or new reproductive partners were not engaged in agonistic interactions with each other. Agonistic interactions were mostly exchanged between individuals of the same sex (Table S3). Males initiated more agonistic behaviours and occupied a more central position within the network than females (Figure 2b; out-$\text{degree}_{\text{males}}$ = 13.79 + 8.03, out-$\text{degree}_{\text{females}}$ = 6.80 + 4.99, eigenvector $\text{centrality}_{\text{males}}$ = 0.17 + 0.05, eigenvector $\text{centrality}_{\text{females}}$ = 0.12 + 0.04). However, receiving agonistic interactions did not vary with sex (Table S4; in-$\text{degree}_{\text{males}}$ = 11.88 + 5.58, in-$\text{degree}_{\text{females}}$ = 9.87 + 5.94). Agonistic interactions occurred mostly between individuals of similar age (Table S3).

Older birds initiated more and received fewer agonistic interactions. However, age did not influence the centrality position occupied within the network (Table S4).

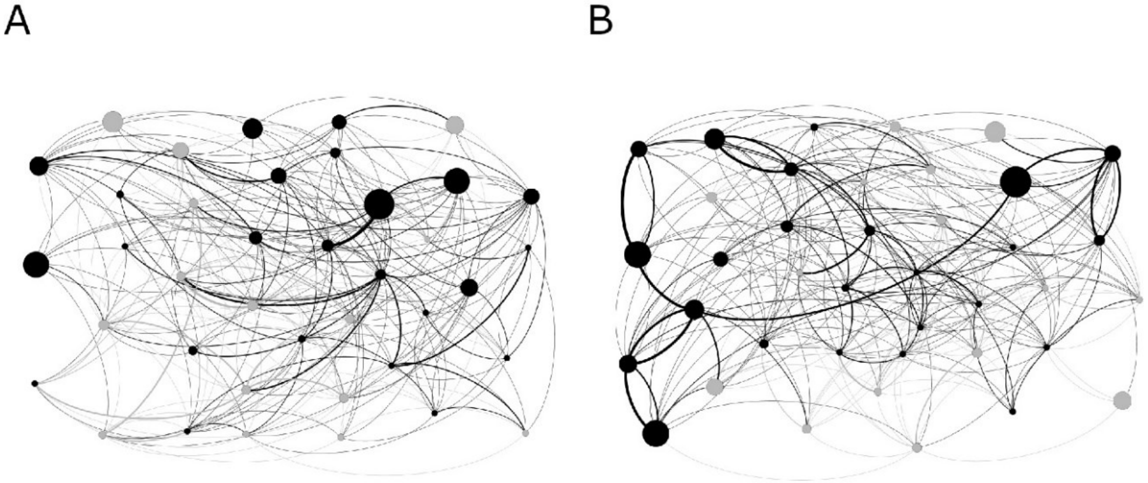

Figure 2. Directed social networks of the initiated and received agonistic interactions in autumn (a) and winter (b). Males are highlighted in black, females in grey. Node size increases with the age of the individuals. Edge size represents how often an individual was involved in an agonistic interaction with another colony member. Edge colour indicates the origin of the behaviour and the direction of the association is shown clockwise. $N_{males} = 24$, $N_{females} = 15$

Affiliative interactions

The affiliative association network deviated from random variation during autumn ($t_{observed} = 3.885$, $t_{permutation\ mean} = 11.937$, $p_{one\text{-}tailed} = 0.002$) and winter ($t_{observed} = 3.843$, $t_{permutation\ mean} = 11.125$, $p_{one\text{-}tailed} = 0.002$). We found effects of season, reproductive partner, age and sex on patterns of affiliative interactions. Generally, more affiliative behaviour was initiated and received during winter than autumn, independent of sex and age. Furthermore, the social centrality position of single individuals within the network did not differ between seasons (Table S2).

Autumn

A network density of 5.2% was found in the affiliative network during autumn. Affiliative interactions were mostly observed between previous and new reproductive partners. All focal animals except for two were involved in affiliative interactions. However, sex-based homophily and age-based heterophily had no influence on the selection of interaction partner (Table S3). We found no sex differences in initiating and receiving affiliative behaviour as well as no effect of sex or age on the individual centrality position within the network (Figure 3a; out-degree$_{\text{males}}$ = 11.71 + 13.94, out-degree$_{\text{females}}$ = 17.73 + 16.81, indegree$_{\text{males}}$ = 11.88 + 14.97, in-degree$_{\text{females}}$ = 17.47 + 16.23, eigenvector centrality$_{\text{males}}$ = 0.03 + 0.14, eigenvector centrality$_{\text{females}}$ = 0.05 + 0.18). Older birds increasingly initiated and received affiliative behaviours (Table S4).

Winter

Similar to autumn, the network density reached 4.7% in the affiliative network during winter, indicating relatively few connections. Affiliative interactions occurred mostly between previous and new reproductive partners. Sex-based homophily and age-based heterophily had no influence on the selection of interaction partner (Table S3). Females received significantly more affiliative interactions than males (Figure 3b; in-degree$_{\text{males}}$ = 19.83 + 26.87, in-degree$_{\text{females}}$ = 38.73 + 34.22). However, initiating affiliative interactions did not vary with sex (out-degree$_{\text{males}}$ = 24.83 + 29.78, out-degree$_{\text{females}}$ = 30.73 + 30.59). Sex and age had no influence on the centrality position occupied within the network (eigenvector centrality$_{\text{males}}$ = 0.03 + 0.14, eigenvector centrality$_{\text{females}}$ = 0.05 + 0.18). Older birds initiated as well as received significantly more affiliative behaviours (Table S4).

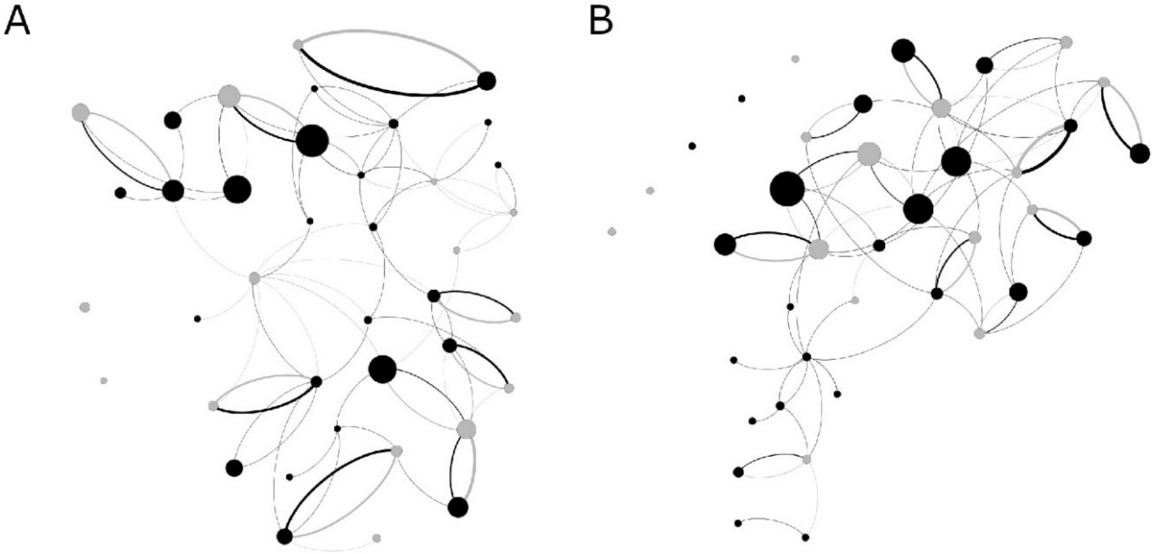

Figure 3. Directed social networks of the initiated and received affiliative interactions in autumn (a) and winter (b). Males are highlighted in black, females in grey. Node size increases with the age of the individuals. Edge size represents how often an individual was involved in an affiliative interaction with another colony member. Edge colour indicates the origin of the behaviour and the direction of the association is shown clockwise. N_{males} = 24, $N_{females}$ = 15

Discussion

In our study we document strong seasonal differences in patterns of proximity and social behaviour in the endangered Northern Bald Ibis. Specifically, we recorded (1) lower interindividual distance (high proximity network density) during autumn compared with winter, (2) no seasonal difference in patterns of agonistic behaviour but more agonistic interactions in males than females, (3) seasonal and sex differences in affiliative behaviour with more affiliative behaviour during winter and more affiliative behaviour received by females than males, (4) reproductive partners as preferred affiliative interaction partners, and (5) an effect of age on social and centrality position within the group, with younger birds being less central in the proximity network and receiving more agonistic interactions.

During winter, individuals associated with fewer other colony members, as shown by the number of associates, but they had stronger connections to specific individuals. Relationship patterns may have changed over time as a consequence of reproductive seasonality (Brent *et al.* 2013) as breeding pair formation starts anew before the onset of the forthcoming breeding season (i.e., already in autumn;

Böhm & Pegoraro 2011). This was also supported by our findings that especially older individuals and reproductive partners (former or prospective mates) were observed in close proximity. Seasonal changes in affiliative interactions may also reflect differences in pair bond stability, with loose bonds during the non-breeding season and stronger bonds during the breeding season (Rowley & Bateson 1985). Furthermore, season-dependent changes in associations could have important implications for conservation: For example, identifying transmission pathways of infectious diseases within an endangered species' population but also between populations (Hamede *et al.* 2009). Contrary to our expectations, the occurrence of agonistic encounters did not differ between seasons, whereas affiliative interactions were more evident during winter. Increased affiliative interactions may indicate a function for pair bond quality and mate familiarity. In fact, there is evidence from socially monogamous Blue-Footed Boobies (*Sula nebouxii*) that affiliative interactions enhance within pair coordination and cooperation during brooding and chick rearing (Sánchez-Macouzet *et al.* 2014).

Sex and age may strongly influence how individuals aggregate and with whom they interact (Boucherie *et al.* 2016; Rose & Croft 2018; Widdig *et al.* 2001). In the present study, patterns of agonistic and also to some extent affiliative interactions differed considerably between males and females during winter. High frequencies of initiated agonistic interactions mostly between males may reflect male-male competition for nest sites. In turn, high frequencies of received affiliative behaviours in females hint at male-male competition for mates. Previous or potentially prospective reproductive partners may invest in pair bond formation and subsequently in pair bond quality with a high exchange of affiliative behaviours. Thus, it seems that, as in other species, males and females have different behavioural patterns during winter, the onset of the breeding season, which may reflect individual investment into pair bond formation and maintenance (Kubitza *et al.* 2015; McGraw *et al.* 2010; Röell 1978). By showing consistent levels of aggressiveness (high or low) individuals may avoid extended fights: Males, for instance, may benefit in male-male agonistic interactions through consistency in their high levels of aggressive behaviours, whereas females may benefit from low levels of agonistic behaviours (Dall *et al.* 2004). Our results further imply that females received affiliative behaviours predominantly from previous or potentially prospective mates.

Partner affiliation may bring significant benefits to both sexes, as socio-positive relationships can be beneficial in terms of lower levels of stress hormones, which may have a positive impact on the immune system (Puehringer-Sturmayr *et al.* 2018) or better access to food and protection against predators (Kalbitzer *et al.* 2017). This suggests that affiliative interactions among Northern Bald Ibis may also be interpreted as an investment of a partner towards containing the potentially detrimental effect of high parasite load on fitness (Frigerio *et al.* 2016), which was shown in Cape Ground Squirrels (*Xerus inauris*; Hillegass *et al.* 2010). In the present study, affiliative interactions frequently occurred between previous or prospective reproductive partners. However, other avian species living in year-round sociality showed different patterns: Rooks (*Corvus frugilegus*), for instance, do not restrict affiliative behaviour to breeding partners (Boucherie *et al.* 2016). Future research could test for the quality of the pair bond or for re-mating occurrence in relation to patterns of affiliative behaviour during the breeding season.

As in other species (mammals: Bekoff 1972; primates: Chalmers 1983; honey bees: Amdam 2011), our findings in Northern Bald Ibis support the idea that social interactions with conspecifics and the individual social role change with age. Stability of relationships can influence how a population reacts to environmental change. For instance, social instability may reduce survival and fitness by increasing inter-individual aggression (Linklater *et al.* 1999). Notably, dispersal decisions might be a consequence of early social experience (Bekoff 1977; Holekamp *et al.* 1984). Up to 50% of the juveniles in the study population disperse, some of which return during autumn (Böhm *et al.* 2020). In our study, young Northern Bald Ibis occupied social positions at the edge of the proximity network; in addition, they received many agonistic interactions and almost no affiliative interactions. Individuals of similar age mainly engaged in agonistic interactions with each other, but there was no evidence of them being in closer proximity or being involved in affiliative interactions with conspecifics of similar age. Thus, juveniles might not have formed socio-positive relationships among themselves.

Different positions within a social network might also be associated with age-related mortality risk and potential fitness consequences. Juvenile Greylag Geese

(*Anser anser*), for example, became more successful as breeders later in life than others if they had higher social connectivity during earlier life stages (Szipl *et al.* 2019). Because juvenile Greylag Geese form long-lasting social bonds with their parents (Rutschke 1982), this may influence reproduction early in life due to the parents' associated social position within the flock (Szipl *et al.* 2019); but this does not apply to Northern Bald Ibis, as offspring do not maintain long-lasting relationships with their parents (Böhm & Pegoraro 2011). As our study shows, juvenile Northern Bald Ibis occupy social positions on the edge of the network and tend to disperse instead of staying.

In addition to the parameters considered in this study (i.e., season, reproductive partner, sex and age), several additional factors could have an impact on patterns of relationships, such as density and distribution of food (Chapman 1990; Howery *et al.* 1998), the presence of peers (Howery *et al.* 1998) or behavioural phenotype (i.e., passive or active; Croft *et al.* 2009). Density and distribution of food, for instance, generally determines group size, as shown for instance in Spider Monkeys (*Ateles geoffroyi*; Chapman 1990). Even though our Northern Bald Ibis population receives supplemental feeding during winter, behavioural observations were not performed in this context; therefore, we tend to exclude such an effect on inter-individual distance (i.e., proximity) or agonistic encounters in the present study. Furthermore, social factors (i.e., peers) can alter location and habitat use by increasing distance or associations to specific individuals (e.g., yearling cattle, Howery *et al.* 1998). Our results suggest that mainly pair partners (former/prospective mates) are involved in establishing social ties. This suggests that colony formation in the Northern Bald Ibis serves mainly predator avoidance and info-parasitism, but is not the basis for cooperation that goes beyond the reproductive pair, whereas Greylag Geese establish female-bonded clans within the flock in addition to the reproductive pair (Frigerio *et al.* 2001). Behavioural traits may also modify an individual's number of ties, as passive individuals may seek refuge in a social group (e.g., Guppies (*Poecilia reticulata*), Croft *et al.* 2009). Regarding the role of individual behavioural phenotype, our unpublished data suggest that passive juveniles are more likely to be in the centre of a social group compared to active juveniles (Puehringer-Sturmayr et al. in prep). We are aware that the aviary conditions might have affected the patterns we observed. Most birds remained at their nest site during winter, probably because of the harsh alpine weather conditions, while the birds freely roamed the foraging grounds throughout the valley during autumn. Aviary size could have led to a concentration of interactions and proximity between colony members in winter. However, as the birds were able to leave the aviary at any point, and we indeed made observations outside the aviary as well, we conclude that the observed patterns of relationships were not fully constrained by the location.

Investigating patterns of relationships in an endangered species is relevant for conservation and reintroduction projects in the wild. The social complexity of a Northern Bald Ibis colony is a challenge when reintroducing individuals (Bowden *et al.* 2010) as the social structure of a released group may have tremendous effects on reproductive success (Böhm & Pegoraro 2011). Our results imply that young Northern Bald Ibis may be less optimal for reintroduction because of greater mortality and dispersal risk associated with their social position within the network than adults. However, in combination with 'human parents' for the chicks, the release of groups of hand-reared Northern Bald Ibis chicks with contact to human parents has been shown to be effective (Jordan *et al.* 2003). From other study systems, there is evidence that the age structure of a released group has an immense effect on survival and fertility (Sarrazin & Barbault 1996); therefore, designing release programs that take into account age-specific bottlenecks to survival and the strengths and limitations of hand rearing should inform approaches. Specifically, understanding the social position of individuals could help to select specific individuals for reintroduction and to predict seasonal trends in habitat use associated with behaviour (Snijders *et al.* 2017), age-related mortality risk associated with different positions within the social network (Ellis *et al.* 2017), and not least the role of male affiliative behaviour for pair bond formation (Kubitza *et al.* 2015).

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Author contributions | DF, VP-S, KK and TS contributed to the study conception and design. Data collection was performed by TS. Data analysis was done by VP-S and TS. The first draft of the manuscript was written by VP-S, TS and DF. SK and KK revised the manuscript, contributed analysis tools, and reviewed drafts of the paper. All authors commented on previous versions of the manuscript and read and approved the final manuscript.

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Compliance with ethical standards

Conflict of interest | The authors declare that they have no conflict of interest.

Ethics | This study was carried out following all current Austrian laws and regulations regarding the work with wildlife. Observing the animals was performed under Animal Experiment Licence Number 66.006/0026-WF/V/3b/2014 by the Austrian Federal Ministry for Science and Research (EU Standard, equivalent to the Animal Ethics Board).

Supplementary Material

Table S1 List of all focal individuals. Name, sex (m=male, f=female), year of hatching and age in month are indicated

Name	Sex	Year of hatching	age in month
Othello	m	1999	212
Hombre	m	2002	176
Abraxas	m	2002	176
Aleppo	f	2006	129
Simon	m	2006	128
Shannara	m	2007	117
Cian	m	2008	105
Schreckse	f	2008	105
North Face	m	2009	92
Sequoia	f	2009	93
Hilda	m	2009	92
Ozzy	m	2010	80
Tiffi	m	2011	69
Lukas	m	2012	57
Kleopatra	f	2013	45
Khan	m	2013	45
Elvis	m	2013	45
Minerva	f	2013	45
Luzifer	m	2014	32
Chicco	f	2014	33
Kira	f	2014	33
Mocha	f	2014	33
Quinto	f	2014	33
Taska	f	2014	33
Smirne	m	2015	20
Simba	m	2015	20
Sandro	f	2015	20
Hurricane	f	2016	9
Ash	m	2016	9
Augustus	m	2016	9
Karma	m	2016	9
Kuzco	m	2016	9
Kalypso	f	2016	9
Draco	m	2016	9

Delilah	f	2016	9
Quasimodo	m	2016	9
Quetzal	f	2016	9
Moriarty	m	2016	8
Mufasa	m	2016	8

Table S2 Results of the Wilcoxon signed rank test with continuity correction. Test statistic, p-values, and additionally mean and standard deviation (SD) in relation to season are given. Significant results are marked in bold

Response variable	**Test statistic V**	***p*-value**	**Season**	**Mean ± SD**
Proximity				
Weighted degree	**0**	**<0.001**	**Autumn**	**33.95 ± 13.00**
			Winter	**60.87 ± 16.89**
Eigenvector centrality	372.0	0.813	Autumn	0.14 ± 0.07
			Winter	0.15 ± 0.07
Agonistic interactions				
Weighted out-degree	261.5	0.385	Autumn	9.95 ± 8.05
			Winter	11.10 ± 7.75
Weighted in-degree	274.5	0.248	Autumn	9.95 ± 5.28
			Winter	11.10 ± 5.73
Eigenvector centrality	327.0	0.383	Autumn	0.14 ± 0.07
			Winter	0.15 ± 0.06
Affiliative interactions				
Weighted out-degree	**118.5**	**<0.001**	**Autumn**	**14.03 ± 15.18**
			Winter	**27.10 ± 29.83**
Weighted in-degree	**185.5**	**0.004**	**Autumn**	**14.03 ± 15.50**
			Winter	**27.10 ± 30.91**
Eigenvector centrality	68.5	0.179	Autumn	0.04 ± 0.16
			Winter	0.04 ± 0.16

Table S3 Coefficients of the Double Dekker Semi-Partialling Multiple Regression Quadratic Assignment Procedure (MR-QAP). Coefficients, including standardized estimates, standard errors (SE), permutation average (i.e. average value of the measure of association), and p-values are given. Significant results are marked in bold

Coefficient	**Estimate**	**SE**	**Permutation average**	**p-value**
Proximity (autumn)				
Intercept	0.000	0.000	0.000	<0.001
Reproductive partner	**0.437**	**0.343**	**-0.019**	**0.001**
Sex-based homophily	0.032	0.099	0.001	0.395
Age-based heterophily	-0.028	0.001	-0.000	0.513
Proximity (winter)				
Intercept	0.000	0.000	0.000	<0.001
Reproductive partner	**0.596**	**0.938**	**-0.061**	**0.001**
Sex-based homophily	0.022	0.242	0.001	0.473
Age-based heterophily	-0.031	0.002	0.000	0.868
Agonistic interactions (autumn)				
Intercept	0.000	0.000	0.000	<0.001
Reproductive partner	-0.010	0.110	0.007	0.651
Sex-based homophily	0.041	0.034	-0.001	0.113
Age-based heterophily	**-0.113**	**0.000**	**0.000**	**0.003**
Agonistic interactions (winter)				
Intercept	0.000	0.000	0.000	<0.001
Reproductive partner	-0.033	0.165	0.007	0.930
Sex-based homophily	**0.091**	**0.050**	**-0.002**	**0.003**
Age-based heterophily	-0.096	0.000	0.000	1.000
Affiliative interactions (autumn)				
Intercept	0.000	0.000	0.000	<0.001
Reproductive partner	**0.680**	**0.719**	**-0.035**	**0.001**
Sex-based homophily	0.000	0.164	-0.006	0.998
Age-based heterophily	-0.010	0.002	-0.000	0.700
Affiliative interactions (winter)				
Intercept	0.000	0.000	0.000	<0.001
Reproductive partner	**0.633**	**1.541**	**0.026**	**0.001**
Sex-based homophily	-0.015	0.348	-0.000	0.624
Age-based heterophily	-0.019	0.003	0.000	0.510

Table S4 Coefficients of the Node-Level Regression. The coefficients, including estimates, beta values, standard errors (SE), t-values and p-values, are given. Significant results are marked in bold

Response variable	Coefficient	Estimate	Beta	SE	t-value	*p*-value
Proximity (autumn)						
Weighted degree	Intercept	26.949	0	3.240		
	Sex (female)	0.250	0.009	3.846	0.065	0.944
	Age	**0.124**	**0.515**	**0.035**	**3.534**	**0.001**
Eigenvector centrality	Intercept	0.105	0	0.017		
	Sex (female)	0.003	0.024	0.020	0.166	0.857
	Age	**0.001**	**0.534**	**0.000**	**3.701**	**0.001**
Proximity (winter)						
Weighted degree	Intercept	56.469	0	4.427		
	Sex (female)	-5.419	-0.158	5.253	-1.031	0.316
	Age	**0.116**	**0.373**	**0.048**	**2.431**	**0.018**
Eigenvector centrality	Intercept	0.117	0	0.018		
	Sex (female)	0.000	0.003	0.022	0.020	0.988
	Age	**0.001**	**0.399**	**0.000**	**2.558**	**0.018**
Agonistic interactions (autumn)						
Weighted out-degree	Intercept	6.314	0	2.079		
	Sex (female)	-0.312	-0.019	2.468	-0.127	0.912
	Age	**0.067**	**0.453**	**0.022**	**2.995**	**0.007**
Weighted in-degree	Intercept	12.104	0	1.130		
	Sex (female)	2.652	0.248	1.341	1.978	0.058
	Age	**-0.057**	**-0.583**	**0.012**	**-4.662**	**0.001**
Eigenvector centrality	Intercept	0.128	0	0.021		
	Sex (female)	0.022	0.151	0.024	0.898	0.367
	Age	0.000	0.101	0.000	0.603	0.560
Agonistic interactions (winter)						
Weighted out-degree	Intercept	10.227	0	1.826		
	Sex (female)	**-5.796**	**-0.368**	**2.167**	**-2.675**	**0.009**
	Age	**0.056**	**0.389**	**0.020**	**2.821**	**0.011**
Weighted in-degree	Intercept	15.579	0	1.376		
	Sex (female)	-3.251	-0.280	1.633	-1.991	0.051
	Age	**-0.058**	**-0.546**	**0.015**	**-3.890**	**0.001**
Eigenvector centrality	Intercept	0.179	0	0.014		
	Sex (female)	**-0.056**	**-0.491**	**0.017**	**-3.295**	**0.003**
	Age	-0.000	-0.131	0.000	-0.883	0.388

Affiliative interactions (autumn)						
Weighted out-degree	Intercept	3.402	0	3.835		
	Sex (female)	8.811	0.286	4.552	1.936	0.062
	Age	**0.130**	**0.462**	**0.041**	**3.129**	**0.005**
Weighted in-degree	Intercept	2.805	0	3.856		
	Sex (female)	8.634	0.275	4.576	1.887	0.065
	Age	**0.142**	**0.495**	**0.042**	**3.398**	**0.002**
Eigenvector centrality	Intercept	0.018	0	0.046		
	Sex (female)	0.021	0.065	0.054	0.381	0.676
	Age	0.000	0.068	0.000	0.402	0.703
Affiliative interactions (winter)						
Weighted out-degree	Intercept	9.967	0	7.849		
	Sex (female)	10.887	0.180	9.315	1.169	0.265
	Age	**0.232**	**0.421**	**0.085**	**2.737**	**0.012**
Weighted in-degree	Intercept	6.961	0	7.982		
	Sex (female)	**23.218**	**0.370**	**9.472**	**2.451**	**0.021**
	Age	**0.201**	**0.352**	**0.086**	**2.330**	**0.035**
Eigenvector centrality	Intercept	0.036	0	0.046		
	Sex (female)	0.018	0.057	0.054	0.338	0.734
	Age	-0.000	-0.020	0.000	-0.120	0.903

For sex, males were set to zero.

PART II

Movement ecology in social animals

CHAPTER III

RESEARCH ARTICLE

Effects of bio-loggers on behaviour and corticosterone metabolites of Northern Bald Ibises (*Geronticus eremita*) in the field and in captivity

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Picture credit: Verena Pühringer-Sturmayr

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NEW DISCOVERY ARTICLE

Tracking birds:
How a little backpack could affect the life of a wild bird

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TRACKING BIRDS: HOW A LITTLE BACKPACK COULD AFFECT THE LIFE OF A WILD BIRD

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Abstract

Background: During the past decades, avian studies have profited from the development of miniature electronic devices that allow long-term and long-range monitoring. To ensure data quality and to inform understanding of possible impacts, it is necessary to test the effects of tagging. We investigated the influence of GPS-transmitters on the behaviour and physiology (levels of excreted corticosterone metabolites, CM) of an endangered bird species, the Northern Bald Ibis (*Geronticus eremita*). We considered effects of GPS-tags in two contexts: (1) aviary (i.e. in captivity), focussing on short-term effects of transmitters on locomotion, foraging and maintenance behaviour (20 individuals that differed in sex and age observed for 10 days) and (2) field, focussing on intermediate-term effects of transmitters on locomotion, foraging, maintenance behaviour, dorsal feather preening, social interactions and physiology (CM) (24 individuals observed for 79 days). In both contexts, focal animals were equipped with bio-logger backpacks mounted with a harness.

Results: In the aviary, behavioural observations were limited to the first days after tagging: no differences were found between individuals with GPS-tags and their controls with respect to the behavioural parameters considered. In the field, no behavioural differences were found between the GPS-tagged individuals and their controls; however, one month after tagging, individuals with GPS-tags excreted significantly more CM than their controls before returning to baseline levels.

Conclusions: Our results suggest that GPS-transmitters did not affect foraging, locomotion and maintenance behaviour in the Northern Bald Ibis in the short or intermediate-term. However, they did affect the hypothalamic-pituitary-adrenal reactivity in the intermediate term for one month before returning to baseline levels the next month. As the Northern Bald Ibis is listed as endangered, evaluating possible adverse effects of bio-logging is also relevant for potential conservation and reintroduction research.

Keywords: short-term effects, bio-tagging, social behaviour, birds, excreted corticosterone metabolites, body weight, maintenance behaviour, middle-term effects, short-term effects

Background

During the past decades, device miniaturization and advancements in battery life have greatly aided researchers in overcoming challenges and constraints for following free-roaming animals (Barron *et al.* 2010; Kays *et al.* 2015). Avian studies, in particular, have benefited from such advances as researchers can now track migratory routes and gain understanding about wintering areas and connectivity in birds (Arlt *et al.* 2013; Bairlein *et al.* 2012; Klaassen *et al.* 2014; Stuchbury *et al.* 2009). The predictive models generated by geographical datasets are of considerable importance for conservation biologists but also for other disciplines, for example, veterinary medicine (Kays *et al.* 2015). Despite these benefits, recent research has emphasized the need to identify any possible effects of GPS-tagging before making inferences about the biology of an animal (Hiraldo *et al.* 1994; Wanless 1992; Wilson & McMahon 2006). Meta-analyses of the impacts of GPS-tags suggest that attaching transmitters and similar devices adversely affects behaviour in a range of bird species (Barron *et al.* 2010). The most substantial effects include increased maintenance behaviour (e.g. preening, fluffing and stretching), restlessness, and energy expenditure as well as decreased likelihood of nesting (Barron *et al.* 2010; Godfrey *et al.* 2003; Mateo-Moriones *et al.* 2012). How potential adverse effects scale with transmitter weight is still not well known (Barron *et al.* 2010 and references therein). It has been suggested that the effects of transmitters weighing less than 5% of the body weight of an animal would only have negligible effects (Brander & Cochran 1969). However, other studies have suggested that it is advisable not to exceed 3% (Phillips *et al.* 2003) – but see Tomotani *et al.* (2019) who conclude that using relative logger weight can be a dangerous assumption in general. McMahon *et al.* (2011) assessed four main categories for describing the potential effects of GPS-tags: (1) those originating from capturing an animal; (2) the type of device, including shape, size and colouration, (3) the method applied for mounting the device; and (4) timing and duration of bio-logging.

The evaluation of the impacts of GPS-tags has animal welfare implications, as some animals may experience a stress response to the device (Möstl & Palme 2002). Physiological parameters such as circulating and/or excreted glucocorticoid levels are usually considered a good indicator of the stress response (Hawkins 2004; Ropert-Coudert & Wilson 2005; Schulz *et al.* 2005). Glucocorticoid levels increase in response to stressful situations. This is an endocrine mechanism that aids adaptive defensive response (Möstl & Palme 2002), but severe chronic stress may have detrimental effects (e.g. reduced reproductive success or impaired memory; Bowman *et al.* 2003; Cyr & Romero 2007). Thus, additionally to behaviour, physiological measurements might be important in assessing the impact of GPS-loggers on target species. Consideration of such parameters can inform whether the deployment of GPS transmitters is a source of stress for the animal (Hawkins 2004; Ropert-Coudert & Wilson 2005; Schulz *et al.* 2005). Because invasive physiological surveys may themselves be stressful (Gessaman & Nagy 1988; Hamilton & Weeks 1985; Maho *et al.* 1992; Roy & Woolf 2001; Schulz *et al.* 1998; Vleck *et al.* 2000), measuring excreted immune-reactive corticosterone metabolites (CM) provides a non-invasive alternative (Ludders *et al.* 2001; Wasser *et al.* 2000; Suedkamp Wells *et al.* 2003). As steroids are metabolised in the liver and excreted into the gut, glucocorticoid metabolite concentrations can be detected in the faeces of mammals or the droppings of birds. Such concentrations have been shown to be representative for the circulating levels (Möstl *et al.* 2005; Palme 2005; Palme & Möstl 1997; Touma & Palme 2005). Suedkamp Wells *et al.* (2003) showed that captive Dickcissels (*Spiza americana*) equipped with bio-loggers in the post-breeding season exhibited elevated CM concentrations in the first 24 hours after tagging. Yet excreted glucocorticoid levels returned to baseline levels within 48 hours after tagging, which was interpreted as indicating no long-term effects of the attached loggers. GPS-equipped black-legged kittiwakes (*Rissa tridactyla*) also showed increased plasma corticosterone levels compared to controls during the early chick rearing phase (Heggøy *et al.* 2015). These findings underscore the need to investigate potential effects of GPS-devices on the physiology and behaviour of study animals.

The aim of this study is to examine the influence of bio-logging on the behaviour and physiological parameters of the Northern Bald Ibis (*Geronticus eremita*). After being listed as critically endangered for many years, this species is now listed as endangered since 2018. Understanding the effects of GPS-transmitters in this system is potentially important for conservation and reintroduction projects (e.g. in Europe and North Africa) that apply telemetry devices for monitoring and research.

We considered the effect of GPS-loggers in two different contexts: (1) a study on Northern Bald Ibis in captivity focussing on short-term effects of GPS-loggers on behaviour (i.e. maintenance behaviour, locomotion, foraging) and (2) a study on free-ranging Northern Bald Ibis focussing on short- and middle-term effects of GPS-loggers on behaviour (i.e. maintenance behaviour, dorsal feather preening, locomotion, foraging) and physiological parameters (i.e. excreted immune-reactive corticosterone metabolites). In both contexts, we expected the strongest effects of the GPS-loggers on behaviour shortly after the tagging procedure, as reported from other studies (Chivers *et al.* 2016; Lamb *et al.* 2017; Lameris & Kleyheeg 2017). We predicted an increase in maintenance behaviour in GPS-tagged individuals compared with handled birds (experienced handling but not the tagging procedure) or control birds (experienced neither handling nor tagging) since the presence of the device can change the position of the feathers and therefore lead to more self-directed behaviour (Enstipp *et al.* 2015). We also expected effects of the GPS-transmitters on locomotion and foraging during the first days after attachment because of the increased energy demand caused by the additional weight of the device (Enstipp *et al.* 2015). In the field, we further tested the effect of the GPS-transmitter on social behaviour (i.e. affiliative and agonistic). In case of a logger effect, we expected GPS-tagged birds to be less engaged in social interactions or even be more frequently a target of agonistic interactions. In addition, excreted immune-reactive corticosterone metabolites were assumed to be elevated in the GPS-tagged and handled birds shortly after attachment of the loggers compared to the control birds. For intermediate-term effects (11 weeks), we predicted that behavioural and physiological values would return to baseline (Quillfeldt *et al.* 2012; Wells *et al.* 2003). Furthermore, we investigated whether the GPS-tag has an effect on the body weight of the focal individuals. We expected GPS-tagged birds to show a reduction in body weight as compared to the handled and control groups, due to the increased energy demand of the additional weight and drag of the transmitter (Enstipp *et al.* 2015).

Material and methods

The aviary context is hereafter presented as “context 1” and the field context as ”context 2”.

Field site and study animals

In coordination with the European Breeding Programme (EEP; Böhm 1999), a free-ranging Northern Bald Ibis colony was established in 1997 at the Konrad Lorenz Research Station (KLF, Grünau im Almtal, Austria; 47°48´E, 13°56´N) by hand-raising zoo-bred chicks (Kotrschal 2007; Tuckova *et al.* 1998). This was the first free-flying Northern Bald Ibis colony northward the Alps after the species became extinct in the 17th century. The aim was to implement basic research to gain know-how for reintroduction and conservation purposes (e.g. Bowman *et al.* 2003; Cyr & Romero 2007; Gessaman & Nagy 1988; Loretto *et al.* 2010; Szipl *et al.* 2014). The year-round free-flying birds are housed in a large aviary approximately 20 x 15 x 7 m (L x B x H) at the Cumberland Wildpark where they are able to flutter around and perform short flights. The birds roam the feeding grounds in the Almtal-region, in a radius of 15km of the aviary, returning for roosting at night and for breeding. Supplementary food (hash made from 1-day-old chicks and beef heart, mixed with insects and soaked dog food) is provided twice a day (0800 and 1500 CET) during winter and early spring when natural resources are limited. The birds are well habituated to the close presence of humans, and each of them is marked with an individual combination of coloured leg rings.

Context 1 – Aviary

In summer 2013, the aviary was locked for this study for 10 days. At the time of data collection, the colony consisted of 70 individuals, including adult and juvenile birds. Focal animals were 20 birds, chosen randomly with respect to sex (11 females, 9 males) and age (10 adults, i.e. from the fourth year of age; 10 juveniles, i.e. the first year after hatching; according to the age classification proposed by Böhm & Pegoraro (2011). Age ranged from 0.5 to 11 years (mean age ± SD = 3.9 ± 3.8). Ten individuals were fitted with GPS transmitters (logger group: $N_{females}$=5, N_{males}=5; mean age ± SD = 3.5 ± 3.9) while 10 served as control (handling group:

$N_{females}$=6, N_{males}=4; mean age ± SD = 3.9 ± 3.9). The list of the focal individuals and their measurements is provided in Table 1a.

Table 1a: Context 1 – Aviary. Name, sex, year of hatching, age class, body weight, experimental group, type of transmitter (1 = Ecotone transmitter 1, weight 28 g; 2 = Ecotone transmitter 2, weight 22 g; 0 = no transmitter), transmitter percentage of body weight and the total duration of video recordings for all focal individuals involved in the study.

Name	Sex	Year of hatching	Age class	Body weight	Experimental group	Trans mitter	Transmitter percentage of body weight	Total duration of video recordings [min]
Kleopatra	f	2013	Juvenile	1170	logger	1	2.39	140
Ferdinand	m	2013	Juvenile	1270	logger	1	2.20	150
Sokrates	m	2013	Juvenile	1200	logger	1	2.33	150
Esmeralda	f	2013	Juvenile	1210	logger	1	2.31	151
Steppenwolf	m	2002	Adult	1190	logger	2	1.85	155
Winnetouch	f	2004	Adult	1140	logger	2	1.93	150
Aleppo	f	2006	Adult	1240	logger	2	1.77	150
Cian	m	2008	Adult	1300	logger	2	1.69	160
Elvis	m	2013	Juvenile	1340	logger	2	1.64	150
Sequoia	f	2009	Adult	1100	logger	2	2.00	150
Kahn	m	2013	Juvenile	1320	handling	0	0	155
Sophokles	m	2013	Juvenile	1140	handling	0	0	150
Bazinga	f	2013	Juvenile	1160	handling	0	0	155
Baghira	f	2013	Juvenile	1070	handling	0	0	150
Hombre	m	2002	Adult	1190	handling	0	0	154
Goran	f	2005	Adult	1150	handling	0	0	160
Loki	f	2006	Adult	1200	handling	0	0	154
Shannara	m	2007	Adult	1220	handling	0	0	160
Schreckse	f	2008	Adult	1170	handling	0	0	158
Babsi	f	2013	Juvenile	1030	handling	0	0	160

Context 2 – Field

At the time of data collection, in fall 2017, the colony consisted of 45 individuals, including adult and juvenile birds. Focal animals were 24 adult birds (10 females, 14 males). Their age ranged from 2 to 18 years (mean age ± SD = 7.1 ± 4.5). The focal individuals were assigned to two experimental groups and a control group (8 individuals per group): (i) Logger group ($N_{females}$=4, N_{males}=4; mean age ± SD = 7.8 ± 5.1), birds were equipped with GPS transmitters and experienced handling procedure; (ii) Handling group ($N_{females}$=3, N_{males}=5; mean age ± SD = 6.6 ± 4.6), birds only experienced handling procedure; (iii) Control group ($N_{females}$=3, N_{males}=5; mean age ± SD = 6.9 ± 4.5), birds were neither equipped with GPS transmitters nor experienced handling procedure. The group assignment was done randomly with respect to sex and age. During the period of data collection, the colony was supplemented with food twice in the morning (0745 and 0945 CET; the total amount of food fed in the morning was identical to the one in the afternoon but split into two feeding situations) and once in the afternoon (1500 CET) to facilitate behavioural observations, which started straight after the first morning feeding, and to prevent the individuals from flying away. The list of the focal individuals and their measurements are provided in Table 1b.

Data collection

Context 1 – Aviary

Data collection was performed from 2 to 12 July 2013 (10 days) and was divided into three phases (Table 2): **phase 1**, a four-day long phase to collect baseline observations from the behaviour of the birds in the aviary; **phase 2**, a two-day long treatment phase (i.e. capturing and equipping); **phase 3**, a further four-day long post-treatment observation phase.

Birds were caught on two consecutive days (phase 2) between 0930 and 1430 CET. Captures were done by hand or by using a hand net and avoiding chasing. Several morphological measurements (including body weight for the present study) were taken for different research purposes from all focal individuals. Weighing of individuals ensured that the transmitter did not exceed 3% of the body weight of the bird (Phillips *et al.* 2003; Table 1a), ranging between 1.6% and 2.4% of the body weight of the single individuals. Ten birds were fitted with a GPS-transmitter. The entire procedure (from catching to releasing) lasted between 15 and 25 minutes per individual (mean handling durations ± SD: handling group = 20.7 ± 3.5, logger group = 20.6 ± 2.4).

Table 1b: Context 2 – Field. Name, sex, year of hatching, start body weight, experimental group, type of transmitter (1 = Ecotone transmitter 1, weight 20 g; 2 = Ecotone transmitter 2, weight 22 g; 0 = no transmitter), transmitter percentage of body weight and end body weight for all focal individuals involved in the study.

Name	Sex	Year of hatching	Start body weight	Experimental group	Transmitter	Transmitter percentage of body weight	End body weight
Othello	m	1999	1340	logger	1	1.49	1360
Aleppo	f	2006	1180	logger	2	1.86	
Cian	m	2008	1330	logger	1	1.50	1350
North Face	m	2009	1260	logger	2	1.75	1290
Tiffi	m	2011	1300	logger	1	1.54	1340
Minerva	f	2013	1250	logger	2	1.76	1230
Kira	f	2014	1185	logger	2	1.86	1250
Taska	f	2014	1170	logger	2	1.88	1200
Hombre	m	2002	1280	handling	0	0	1370
Simon	m	2006	1360	handling	0	0	1330
Schreckse	f	2008	1320	handling	0	0	1350
Lukas	m	2012	1340	handling	0	0	1480
Kleopatra	f	2013	1330	handling	0	0	1210
Khan	m	2013	1370	handling	0	0	1430
Chicco	f	2014	1350	handling	0	0	1410
Smirne	m	2015	1370	handling	0	0	1390
Abraxas	m	2002	-	control	0	0	-
Shannara	m	2007	-	control	0	0	-
Hilda	m	2009	-	control	0	0	-
Sequoia	f	2009	-	control	0	0	-
Ozzy	m	2010	-	control	0	0	-
Mocha	f	2014	-	control	0	0	-
Simba	m	2015	-	control	0	0	-
Sandro	f	2015	-	control	0	0	-

Table 2: Phases of the data collection.

Phases	Context 1 – Aviary	Context 2 – Field
Phase 1	a four-day long pre-treatment observation phase; July	an eleven-day long pre-treatment data collection phase; October till November
Phase 2	a two-day long treatment phase (i.e. capturing and equipping); July	a one-day long treatment phase (handling procedure and transmitter attachment); November
Phase 3	a four-day long post-treatment observation phase; July	a ten-day long post-treatment data collection phase; November
Phase 4	-	a five-day long post-treatment data collection phase one month later; December
Phase 5	-	a five-day long post-treatment data collection phase two months later; January

Context 2 – Field

Behavioural data and individual droppings for excreted CM were collected from 25 October 2017 to 11 January 2018 (79 days). Data collection was divided into five phases (Table 2): **phase 1**, an eleven-day long pre-treatment phase to collect baseline behavioural observations and physiological measurements; **phase 2,** a one-day long treatment phase (handling procedure and transmitter attachment); **phase 3**, a ten-day long post-treatment data collection phase; **phase 4**, a five-day long post-treatment phase to perform data collection one month later; **phase 5**, a five-day long post-treatment phase to perform data collection two months later. During phase 2, only droppings for CM analysis were collected; behavioural observations did not take place, as the GPS-transmitters were attached in the morning.

Birds (logger and handling groups) were caught on one day (phase 2) between 0815 and 1100 CET. Captures were done by hand or by using a hand net and avoiding chasing. Body weight was taken as a morphological measurement on the day of transmitter attachment (phase 2) and at the end of the experiment (phase 5). Weighing of individuals ensured that the transmitter did not exceed 3% of the body weight of the birds (Phillips *et al.* 2003; Table 1b), ranging between 1.49% and 1.88% of the body weight of the single individuals (Phillips *et al.* 2003). For further statistical analysis, we calculated the weight change (∆body weight) between phase 2 and phase 5. Eight ibises were fitted with a GPS-transmitter. The entire procedure (from catching to releasing) lasted between 13 and 30 minutes per individual (mean handling durations ± SD: handling group = 18.6 ± 4.7, logger group = 19.6 ± 4.0).

Transmitter attachment

Focal animals of the logger group of both contexts (i.e. in captivity and in the field) were fitted with telemetry devices (Ecotone® Telemetry, Sopot, Poland; http://ecotone-telemetry.com/en), which were backpack-mounted with a harness following an earlier study by (Lindsell *et al.* 2009, see also Table 1a and 1b). All birds were equipped with either GSM-GPS transmitters, which store the GPS locations and transmit them via GSM network to a server, or UHF-GPS transmitters, from which stored GPS-data can be downloaded via UHF-antenna. All loggers were equipped with solar panels to recharge the batteries.

Context 1 – Aviary

Four birds were equipped with GSM-GPS transmitters (Ecotone transmitter 1: weight 28 g, approximately 2.3% of the body weight of the birds ranging between 1170 g and 1270 g; Table 1a). Six ibises were outfitted with UHF-GPS transmitters (Ecotone transmitter 2: weight 22 g, approximately 1.8% of the body weight of the birds ranging between 1100 g and 1340 g; Table 1a).

Context 2 – Field

All focal birds in the logger group were equipped with GSM-GPS transmitters (Ecotone transmitter 1: weight 20 g, approximately 1.5% of the body weight of the birds ranging between 1300 g and 1340 g; Ecotone transmitter 2: weight 22 g, approximately 1.8% of the body weight of the birds ranging between 1170 g and 1260; Table 1b).

In both contexts, the loggers were not removed from the focal individuals after data collection for approximately further eight months; however, logistical and organisational issues did not allow to further investigate the effects of the deployment.

Behavioural data

Context 1 – Aviary

During the eight days of phase 1 and 3, every focal individual was video-recorded (Canon Legria FS306) for 10 minutes twice per day, in the morning between 0900 and 1300 CET and in the afternoon between 1300 and 1800 CET, considering a break of at least two hours between repeated observations of the same individual. In total, 16 protocols were collected per individual, adding up to a sum of 3000 minutes of observation. Due to technical problems some videos of phase 3 got partly lost (on average 6.9 minutes per individual). This was taken into account in the analysis. Videos were analysed using the software Solomon Coder beta (© 2013 András Péter). The following behavioural parameters were coded and analysed: duration of locomotion (including walking and flying), frequency of foraging (including drinking, feeding and poking with the bill in the soil), and frequency of maintenance behaviour (including preening, scratching, shaking, stretching, bathing in the sun or in the water; for an exhaustive description of the ethogram of the Northern Bald Ibis see Pegoraro 1992). Videos were coded by JG and ML after calculation of inter-observer reliability using Kappa statistics (Kappa = 8.3, “almost perfect agreement”; Viera & Garrett 2005).

Context 2 – Field

During phases 1, 3, 4 and 5 behavioural observations of focal individuals were collected with the software Prim8 Mobile (mobile computing to record nature, http://www.prim8software.com/; McDonald & Johnson 2014) by applying focal sampling with a continuous recording method (Altmann 1974; Martin & Bateson 2007). All observations were taken once per day between 0830 and 1200 CET, with each protocol lasting 5 minutes per individual. The simultaneous observation of pair partners was avoided to prevent pseudo-replication in social interactions. In total, 719 protocols were collected (on average: x̅ ± SE = 30 ± 2 focal observations per individual). The following behavioural parameters were coded and analysed: duration of maintenance behaviour (including preening, scratching, shaking, fluffing, stretching, sleeping, resting, bathing in the sun or water), dorsal feather preening (preening the area around the logger), locomotion (walking, short distance flights with the focal individual still in sight) and foraging (drinking, feeding, poking with the bill in the soil), as well as frequency of initiated and received affiliative (i.e. greeting, preening, preening invitation, mutual bill shaking, contact sitting) and agonistic (i.e. displacing, threatening, pecking, fighting) interactions (for an exhaustive description of the ethogram of the Northern Bald Ibis see Pegoraro 1992). Behavioural data were collected by VP-S and TC after calculation of inter-observer reliability using intraclass correlation coefficient (package “irr”, Gamer *et al.* 2012; coefficient = 0.953, “excellent reliability”, Koo & Li 2016). A ratio per minute was calculated for the durations and the frequencies.

Collection of droppings and analysis of corticosterone metabolites

Context 2 – Field

To determine concentrations of excreted CM, individual droppings were collected. Droppings represent an integrated, proportional record of the plasma corticosterone levels depending on the gut passage time (Palme & Möstl 1997), which we know to be 2-3 hours (Puehringer-Sturmayr *et al.* 2018), similar to the records on white ibises (*Eudocimus albus,* Adams *et al.* 2009). Daily sample collection was conducted independently of behavioural observations. To account for possible endogenous diurnal variations, droppings were collected from 1600 to 2000 (CET) each day. The collected sample was transferred into an individual Eppendorf ® microtube (Eppendorf®, Hamburg, Germany) directly after defecation of the focal bird to avoid cross-contamination with other droppings. The samples were stored on ice during collection and within 3 hours frozen at -20 °C for CM analysis. In total, we collected 591 droppings for CM determination (on average: x̅ ± SE = 25 ± 3 droppings per individual).

The analysis was done via an enzyme immunoassay (EIA; Möstl *et al.* 2005; Palme *et al.* 2005; Palme & Möstl 1997) suitable for Northern Bald Ibises

(Puehringer-Sturmayr *et al.* 2018) at the laboratory of the Department of Behavioural Biology, University of Vienna (Austria). The intra- and interassay coefficients of variance amounted to 9.57% and 5.54% respectively.

The measured value of nanogram CM concentration per gram dropping was taken into further statistical analysis.

Statistical analyses

All statistical analyses were carried out using the software R 3.4.0 (R Core Team 2019) and the packages “lme4” (Bates *et al.* 2015), “glmmADMB” (Fournier *et al.* 2012) and “MuMIn” (Barton 2016, 2020). We checked whether the residuals were normally distributed through visual inspection and a Shapiro Wilk test. We used an information-theoretic approach and calculated all possible candidate models, ranked them according to their AICc values (second-order form of Akaike’s information criterion to account for small sample sizes; Hurvich & Tsai 1989) and selected the models with ∆AICc ≤ 2 with respect to the top-ranked model for model averaging in order to create model-averaged coefficients (Burnham & Anderson 2002).

Context 1 – Aviary

We defined (1) locomotion, (2) foraging and (3) maintenance behaviour as dependent variables. Generalized linear mixed models (GLMM) were used to investigate whether phase 2, i.e. the two days of catching and fitting the birds with GPS-transmitters, had an effect on the behavioural categories. In each set of candidate models the frequency or proportion of one behavioural category served as dependent variable with the following fixed factors in each full model: phase (pre- or post-catching), relative weight of the GPS-transmitter (i.e. percentage of the body weight of the individual; for the handled birds this was zero), sex and age class (adult, juvenile), time of day (i.e. morning and afternoon). We included the phase (i.e. 1 or 3) and the relative weight of the transmitter as interaction. Regarding locomotion, we fitted a beta distribution (link = logit); i.e. locomotion was measured as the proportion of observation time. The dependent variable “foraging” contained 133 zeros, and the remaining 170 values varied widely; therefore, it was converted into a binary variable, i.e. foraging or not foraging (family = binomial, link = logit). A negative binomial distribution (link = log) was fitted on the dependent variable “maintenance behaviour” (frequency). The identity of the individual and the day of observation (1 to 8) were added as random factors to all models.

Context 2 – Field

The following parameters were defined as response variables: (1) behaviour (including maintenance behaviour, dorsal feather preening, locomotion, foraging, social interactions), (2) CM and (3) ∆body weight. Behavioural categories were treated as separate dependent variables in the candidate models. Fixed factors in each full model were experimental group, phase and the interaction term between those two parameters. Sex was not included as a fixed factor, as no effect was found in context 1 regarding logger attachment. Subject identities were included as random factors in all models to control for between subject variation and unbalanced design. GLMMs with an inverse gaussian distribution (link = log) were used to assess the effect of GPS transmitter attachment on behaviour. As the inverse gaussian distribution is only able to run with positive values (>0), we added the number 1 to each behavioural category. To investigate the effect on CM and ∆body weight, we used Linear mixed-effects models.

Results

Context 1 - Aviary

Locomotion. Age class was the most important predictor, i.e. juveniles moved more than adults (Additional file 1: Table S1 and Table S2). Compared to age class, the relative importance of pre/post-catching (i.e. phase 1 and 3), time of day and sex was very low; thus, these factors had a less important effect on locomotion (Additional file 1: Table S2). The interaction term was not included in the top-ranked models (Additional file 1: Table S1). Most importantly, the relative weight of the GPS-transmitters did not occur in the best models; accordingly, the presence and weight of a transmitter were not found to affect the behaviour.

Foraging. Age class and time of day were the most important predictors, i.e. juveniles were more likely to forage than adults; foraging was more likely to be observed in the afternoon than in the morning (Additional file 1: Table S2). Compared to age class and time of day, all other parameters (i.e. sex, pre/post-catching and relative transmitter weight) had a much lower relative importance and therefore there is little evidence that these factors influenced foraging (Additional file 1: Table S2). The interaction term was not included in the top-ranked models (Additional file 1: Table S1).

Maintenance behaviour. Time of day was the most important predictor, i.e. in the afternoon maintenance behaviour was observed more frequently (Additional file 1: Table S2). The factor sex also had relatively high importance with 0.82, i.e. females showed less maintenance behaviour than males. The other parameters pre/post-catching, relative transmitter weight and age class all had very low relative importance, meaning that there is little evidence in this dataset that these fixed factors influenced the frequency of maintenance behaviour (Additional file 1: Table S2). The interaction term was not included in the top-ranked models (Additional file 1: Table S1).

Context 2 – Field

Locomotion, foraging and maintenance behaviour. Phase (i.e. the different phases of the data collection) was the most influential variable regarding the response variables maintenance behaviour, dorsal feather preening, locomotion, foraging (Additional file 2: Table S3 and Table S4). Locomotion and foraging (Figure 1) declined throughout phases 1 to 4 and showed an increase in phase 5. The duration of dorsal feather preening only slightly changed during the experiment, whereas a peak in maintenance behaviour was observed in phase 4 (five-day-long post-treatment phase one month later) with decreasing durations in phase 5 (five-day-long post-treatment phase two months later; Figure 1). Experimental group and the interaction term were not included in the top-ranked model.

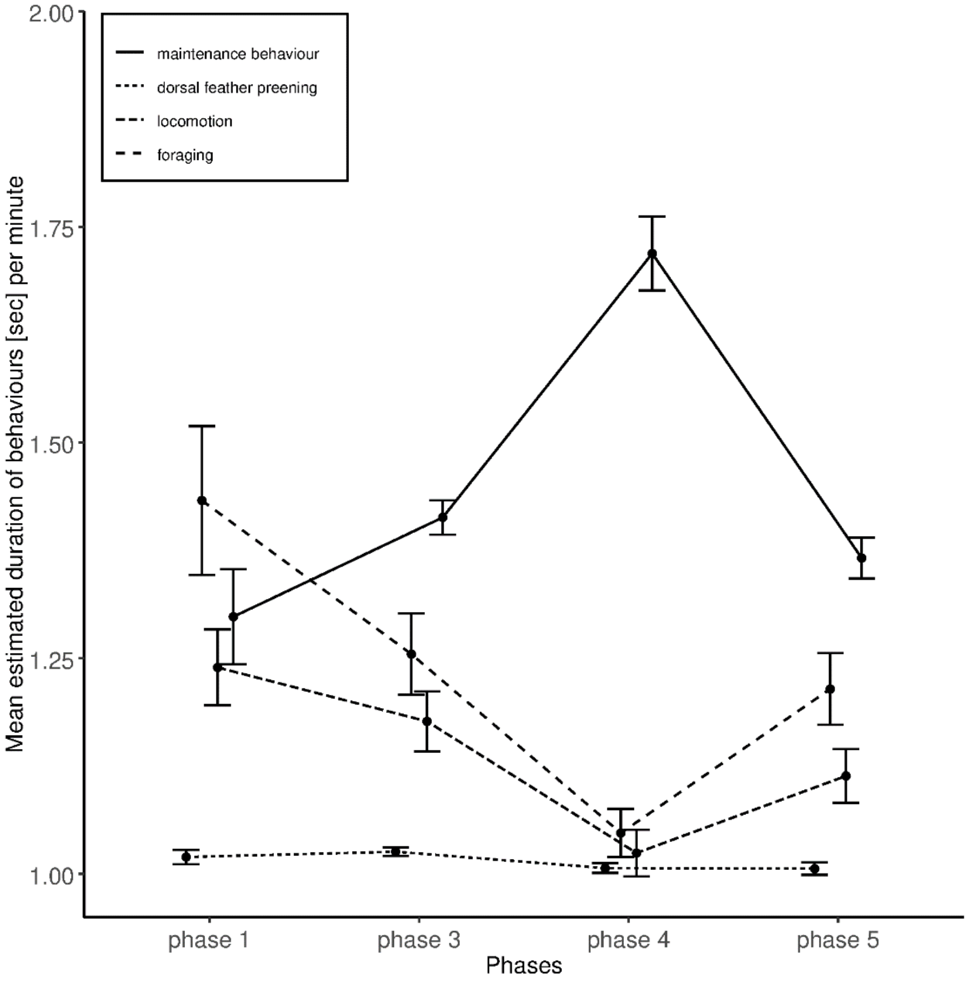

Figure 1. Context 2 - Field. Mean estimated durations [sec] per minute of locomotion, foraging, maintenance behaviour as well as dorsal feather preening. For a detailed description of the phases, see Table 2. Solid line = maintenance behaviour, dashed line = dorsal feather preening, dotted line = locomotion, dotdash = foraging. N=24.

Social behaviour. Model averaged results identified phase, experimental group and the interaction term between the two parameters as the strongest determinant of initiated and received affiliative behaviour (Additional file 2: Table S3 and Table S4). The affiliative behaviours (initiated and received) increased initially in the GPS-tagged birds compared with the handled and control birds; then we observed a decline in the GPS-tagged birds during phase 4. Furthermore, birds in the control (initiated affiliative behaviour) and handled (initiated and received affiliative behaviour) groups showed a peak during phase 3 and 4, respectively; in both cases, the frequencies decreased afterwards (Figure 2 and 3). Received agonistic behaviour was best explained by phase, with decreasing frequencies throughout phases 1 to 4 and increasing during phase 5 (Additional file 2: Table S3 and Table S4). Experimental group and the interaction term were not included in the top-ranked model. Candidate models with initiated agonistic behaviour as response variable did not improve penalised model fit over the null model, as assessed by AICc, indicating that variation in the data cannot be explained by any of the fixed factors.

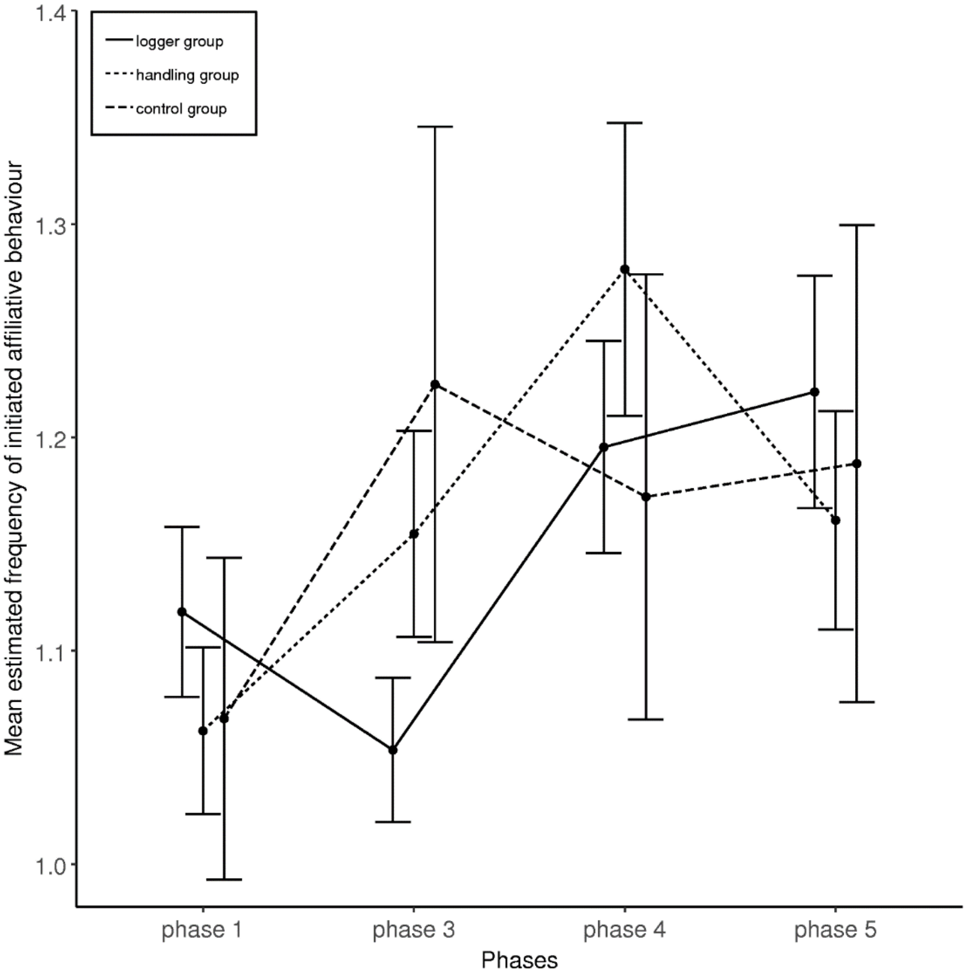

Figure 2. Context 2 – Field. Mean estimated frequency of initiated affiliative behaviour in relation to the different phases and experimental groups. For a detailed description of the phases, see Table 2. $N_{LoggerGroup}$=8, $N_{HandlingGroup}$=8, $N_{ControlGroup}$=8.

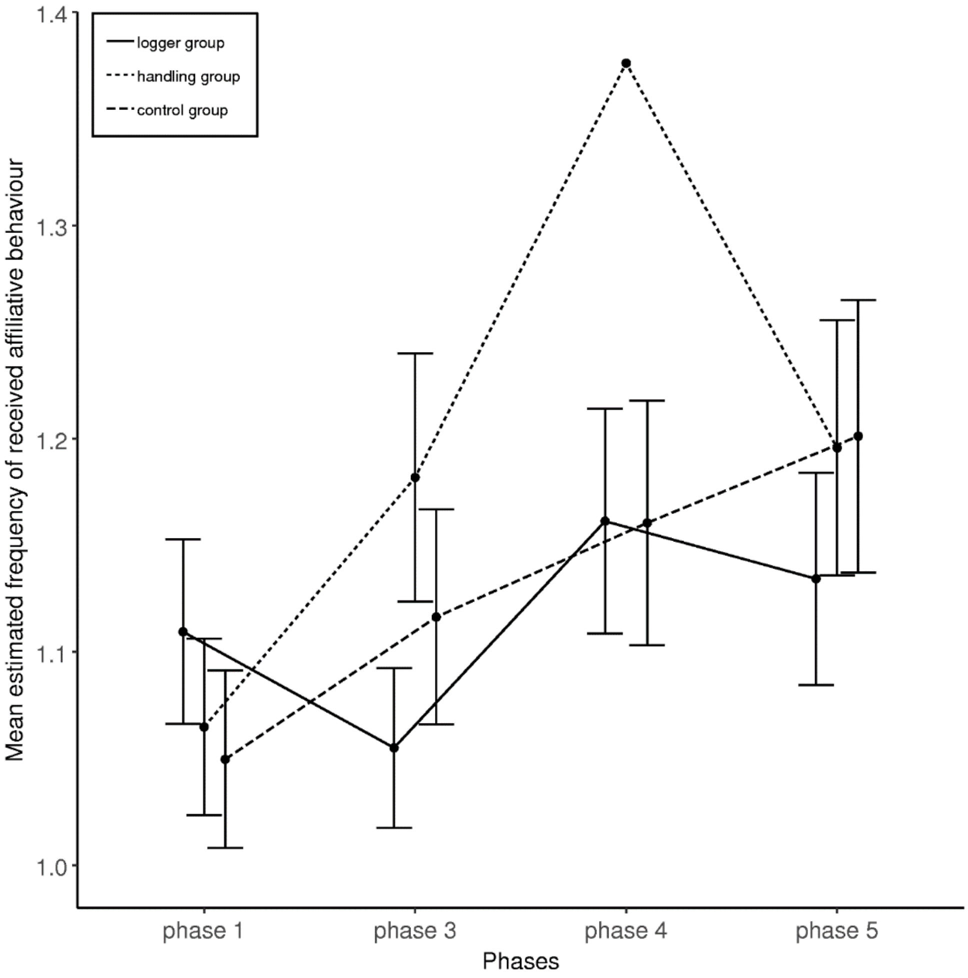

Figure 3. Context 2 – Field. Mean estimated frequency of received affiliative behaviour in relation to the different phases and experimental groups. For a detailed description of the phases, see Table 2. $N_{LoggerGroup}$=8, $N_{HandlingGroup}$=8, $N_{ControlGroup}$=8.

Corticosterone metabolites. The excretion pattern of CM was best explained by phase, experimental group and the interaction term of these fixed factors (Additional file 2: Table S3 and Table S4). CM levels of the GPS-tagged birds increased steadily after GPS-transmitter attachment, whereas a decline was observed within the handled birds (Figure 4). On the contrary, the control birds showed first an increase in CM levels during phase 3, with decreasing levels afterwards. However, during phase 5, all three experimental groups showed similar CM concentrations.

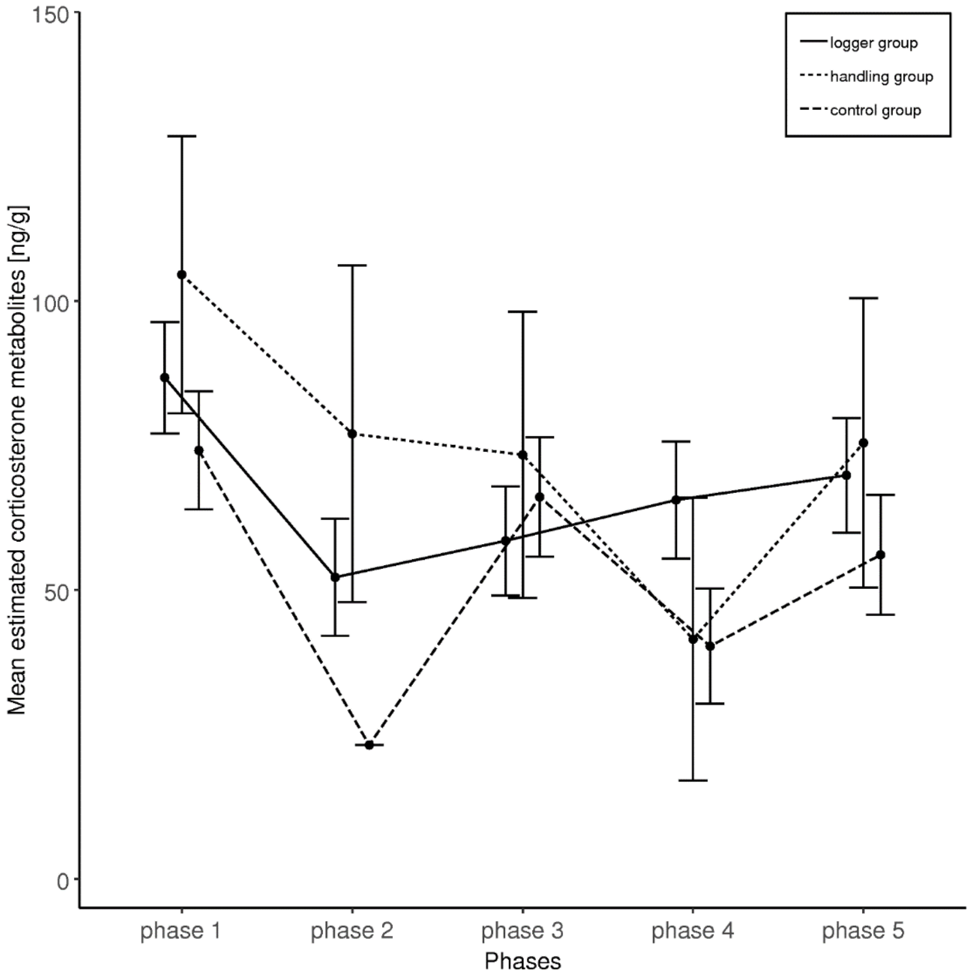

Figure 4. Context 2 – Field. Mean estimated CM [ng/g] in relation to the different phases and experimental groups. For a detailed description of the phases, see Table 2. $N_{LoggerGroup}$=8, $N_{HandlingGroup}$=8, $N_{ControlGroup}$=8.

ΔBody weight. The full model did not improve penalised model fit over the null model, as assessed by AICc, indicating that variation in the data cannot be explained by any of these factors.

Discussion

The deployment of GPS-transmitters on Northern Bald Ibises did not cause remarkable changes in measured behaviour. However, excreted corticosterone metabolites (CM) increased after transmitter attachment during month two before returning to baseline levels during month three. Our results indicate that the GPS-transmitters used in the present study (i.e. up to approximately 2.5% of the body weight of an animal) did not affect foraging, locomotion, maintenance behaviour and dorsal feather preening or received agonistic behaviour in captive and free-flying Northern Bald Ibises during the immediate post-tagging period. The pre- and post-catching phase as well as the relative GPS-transmitter weight in aviary birds (context 1) and the variable “experimental group” in the field (context 2) had no or only low relative importance as compared to other factors such as age class, time of day (context 1) or phase (context 2). These outcomes contradict our expectations, as we expected to find the strongest differences between tagged birds and handled and control birds shortly after catching and tagging. In regard to the aviary study (context 1), perhaps behavioural acclimatisation after logger attachment was facilitated compared to free-flying conditions, as not much energy had to be expended for foraging activities. Both weather conditions and GPS transmitters have been shown to affect the energy costs of behaviour (Elliott *et al.* 2014; Enstipp *et al.* 2015). Such constraints can be reflected in elevated cost of foraging (Heath & Gilchrist 2010) or in behavioural response that minimises such costs (Drent & Daan 1980). Because locomotion, foraging and maintenance behaviour in free-flying Northern Bald Ibis did not seem to be affected by logger deployment in general, we may conclude that the harness-attached GPS-transmitters in the present study did not have a negative impact on the behaviour observed. Furthermore, we can likely exclude a possible effect of handling time, as the mean values of procedure duration were similar between the experimental groups.

Despite the overall finding of little measurable effect of the GPS-transmitter on behaviour, affiliative behaviour decreased in the GPS-tagged group after the attachment as compared to the handled and control groups, indicating that the tagged birds experienced some impact after logger deployment. Even though we did not investigate the social network (Farine & Whitehead 2015) of these birds, one possible explanation for the observed pattern is that GPS-tagged birds moved towards the edge of the network for a short period, and for this reason they initiated and received less affiliative behaviour compared with birds in the handled and control groups. Such behavioural responses could negatively impact reproductive behaviour as breeders are usually better embedded in the social network as compared to non-breeders (Czerny 2018), but this remains to be tested. One of the most substantial effects of GPS-tagging reported in other studies is the decreased likelihood of nesting (Barron *et al.* 2010). A meta-analysis found the strongest negative effects on reproduction in individuals tagged with neck collars (Bodey *et al.* 2018). As we found a clear difference between the handled group and the GPS-tagged group, we can conclude that the observed effect was caused by the logger deployment alone and not due to the handling experience. We can further exclude CM levels as a reason for the decline in affiliative behaviour, as the GPS-tagged group excreted similar concentrations as the handled and control birds during phase 3. Even though the behavioural effect was not long-lasting, a careful consideration of the type and period (i.e. reproductive vs non-reproductive period) of GPS-logger attachment is pertinent.

Our results hint at an effect of GPS-loggers on CM excretion. During phases 1 to 3, all experimental groups showed similar patterns in CM levels. The low value in the control group during phase 2 could be related to the small sample size, resulting in the differences in CM concentrations between the groups. As a seasonal effect, CM levels generally decrease in late fall and increase again towards the onset of the mating season (Hirschenhauser 1998); however, this was not the case during phase 4 (December) in the GPS-tagged birds as compared to the handled and control birds. Notably, the CM concentrations in all three experimental groups were comparable at the end of the experiment (January), and therefore this might be considered a mid-term effect of GPS-tagging. A seasonal or handling effect on CM level can be excluded as the GPS-tagged birds showed an increase in CM concentrations, whereas the handled birds showed similar values to the control group. Further, we can exclude an impact of the GPS-logger deployment on CM due to sex or age, as those parameters were taken into account when designing the experimental setup. The impact of the GPS-loggers on CM could be a consequence of our small sample size. However, we accounted for this possibility when defining and choosing the statistical models. Thus, we tend to exclude this possibility, even though confidence in the pattern would benefit from a greater sample size generating more robust results. Glucocorticoid concentrations have been shown to increase with handling time (Sockman & Schwabl 2001). Therefore, we cannot exclude a possible effect of individual differences in reacting to stressful situations; for instance, small differences in handling time between individuals might have affected the results. Furthermore, we also cannot exclude potential impacts on the flight performance of the GPS-tagged birds as we did not measure flight behaviour.

A recent study showed that flight speed reduces depending on how heavy the bird is after tagging (Tomotani *et al.* 2019), which would certainly have an impact on wild birds. Thus, a more thorough consideration of flight performance would be necessary. Still, the detected effect in the GPS-tagged birds could have consequences for their subsequent reproductive success, due to the possible increase in energy expenditure during the winter period. Under natural conditions such increased energetic expenditure during winter could eventuate in less available energy allocated to reproduction, i.e. building a nest, producing eggs and raising chicks. We did not detect changes in body weight in relation to logger deployment in the present study, and therefore one could argue that GPS-tagged individuals in this study had enough energy available for survival and investment into the breeding season.

Compared to the adult birds, juveniles showed more locomotion and foraging behaviour. Both foraging and maintenance behaviours occurred more often in the afternoon than in the morning, which was independent of the presence of a GPS-transmitter. Thus, when testing the effects of GPS-loggers in animals, it is important to account for different age classes and time of day that could mask variation caused by transmitter effects. A detailed discussion of these results is beyond the scope of this study. However, there is evidence from other studies that juvenile and sub-adult birds had lower foraging efficiency compared with adults and experienced individuals, which may force juveniles to migrate later than adults (Lindsell *et al.* 2009, 2011). In our study, yearling juvenile birds were observed foraging more frequently than adult birds, irrespective of being equipped with a transmitter or not. The hierarchy within the colony is another factor worth considering: sub-adults and especially juveniles after fledging (as in our case) are low in rank and often get displaced by adult birds, who pose a risk to scrounge their food (Pegoraro 1992; Sorato & Kotrschal 2006). Thus, age and time of day can have significant effects that require scrutiny per study species when tagging is considered.

Conclusions

This study was performed on a globally endangered species, for which the kind of data that can be collected by GPS telemetry could be essential to manage its conservation. For example, GPS technology is used to monitor endangered species, their threats and to protect their habitats (Berger-Tal & Lahoz-Monfort 2018) or to detect poaching events (O'Donoghue & Rutz 2016). At the same time, given the small population size, individual birds of this species are disproportionally important for reproduction. For both reasons, it is highly relevant to identify and minimise potential effects of GPS loggers on this species. In the present study, we found no long-term effects of GPS-transmitters below 3% of the body weight of an animal on locomotion, foraging, maintenance and agonistic behaviour in the Northern Bald Ibis. However, affiliative behaviour and the excretion pattern of CM were temporarily affected by tagging. Our results imply that a closer look at physiological parameters is important to detect whether there is an effect on the stress level of the GPS-tagged animals, even though no behavioural changes might be observed after logger deployment. These findings are relevant for conservation and management projects running on species that include the use of animal-carried bio-loggers.

List of Abbreviations

AIC: Akaike's Information Criterion
CI: Confidence Interval
CM: Excreted Immune-Reactive Corticosterone Metabolites
EEP: European Breeding Programme
EIA: Enzyme Immunoassay
GLMM: Generalised linear mixed models
GSM: Global System for Mobile Communications
GPS: Global Positioning System
KLF: Core facility "Konrad Lorenz Research Centre" for Behaviour and Cognition, University of Vienna.
SD: Standard Deviation
SE: Standard Error

UHF: Ultra High Frequency

Declarations

Ethics approval and consent to participate | Not applicable: the study does not involve humans. All authors adhered to the ‘Guidelines for the use of animals in research’ as published in Animal Behaviour (1991, 41, 183–186). This study complies with all current Austrian laws and regulations concerning work with wildlife. The experimental setup was performed under Animal Experiment Licence Numbers BMWFW-66.006/0011-WF/II/3b/2014 and BMWFW-66.006/0026-WF/V/3b/2014 by the Austrian Federal Ministry for Science and Research. We confirm that the owner of the land, the Duke of Cumberland, gave permission to conduct the study on this site. Birds were habituated to the presence of humans.

Consent for publication | Not applicable.

Availability of data and material | The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests | All authors have seen the final manuscript and take responsibility for its content. The authors have no conflict of interest to declare.

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Authors' contributions | DF, JH, MCL and VP-S conceived the study. JG, ML collected the data and analysed the videos for context 1, VP-S and TC collected the data for context 2. MCL and VP-S performed statistical analyses. DF, VP-S, ML, JG, MCL, JH, KK, TC wrote the paper, with DF, VP-S and MCL providing major contributions. All authors read and approved the final manuscript.

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Additional files

Additional file 1: Table S1 and Table S2 [.docx]. Context 1 – Aviary. Top-ranked models form the generalized linear mixed models and model-averaged coefficients (full-model averaging).

Additional file 2: Table S3 and Table S4 [.docx]. Context 2 – Field. Top-ranked models from the linear mixed effects models and generalized linear mixed models as well as model-averaged coefficients of final models.

Additional files

Table S1: Context 1 – Aviary. Top-ranked models from the generalized linear mixed models examining factors influencing the behavioural categories locomotion, foraging and maintenance behaviour. The individual identity and the day were fitted as random factors. ΔAICc = differences of the second order Akaike's Information Criterion between the best model and the other top-ranked models, logLik = log-likelihood.

Response variable	**Model**	**ΔAICc**	**logLik**	**Akaike weight**
Locomotion	Age class	0	558.86	0.40
	Age class+Pre/Post-catching	0.69	559.56	0.28
	Age class+Daytime	1.81	559.00	0.16
	Age class+Sex	1.92	558.94	0.15
Foraging	Age class+Daytime+Sex	0.00	-179.82	0.18
	Age class+Daytime	0.14	-180.93	0.17
	Age class+Daytime+Sex+Pre/Post-catching	0.74	-179.14	0.13
	Age class+Daytime+Relative transmitter weight	0.82	-180.23	0.12
	Age class+Daytime+Sex+Relative transmitter weight	0.85	-179.20	0.12
	Age class+Daytime+Pre/Post-catching	0.89	-180.27	0.12
	Age class+Daytime+Pre/Post-catching+Relative transmitter weight	1.61	-179.58	0.08
	Age class+Daytime+Sex+Pre/Post-catching+Relative transmitter weight	1.63	-178.53	0.08
Maintenance behaviour	Daytime+Sex	0.00	-943.22	0.34
	Daytime	1.28	-944.91	0.18
	Daytime+Sex+Pre/Post-catching	1.30	-942.82	0.18
	Daytime+Sex+Relative transmitter weight	1.50	-942.92	0.16
	Daytime+Sex+Age class	1.84	-943.10	0.14

Table S2: Context 1 – Aviary. Model-averaged coefficients (full-model averaging) with adjusted standard errors (SE), lower and upper limits of the confidence intervals (CI) and the relative importance of the final models explaining the effects on the three behavioural categories, locomotion, foraging and maintenance behaviour.

Response variable	Coefficients	Estimate	Adjusted SE	CI lower limit (2.5%)	CI upper limit (97.5%)	Relative importance
Locomotion	Intercept	-2.40	0.15	-2.69	-2.10	
	Age class	0.61	0.12	0.37	0.84	1.00
	Pre/post-catching	0.06	0.14	-0.13	0.57	0.28
	Daytime	0.01	0.05	-0.17	0.29	0.16
	Sex	0.01	0.05	-0.19	0.28	0.15
Foraging	Intercept	-0.95	0.31	-1.56	-0.34	
	Age class	1.79	0.27	1.26	2.32	1.00
	Sex	0.19	0.27	-0.13	0.89	0.41
	Daytime	0.55	0.26	0.04	1.05	1.00
	Pre/post-catching	0.12	0.22	-0.21	0.80	0.51
	Relative transmitter weight	-0.05	0.11	-0.34	0.09	0.40
Maintenance behaviour	Intercept	2.08	0.10	1.89	2.26	
	Sex	-0.14	0.11	-0.36	0.01	0.82
	Daytime	0.25	0.09	0.07	0.43	1.00
	Pre/post-catching	0.01	0.05	-0.10	0.27	0.18
	Relative transmitter weight	0.00	0.02	-0.11	0.05	0.16
	Age class	-0.01	0.04	-0.23	0.14	0.14

For age class, adults were set to zero.

For pre/post-catching, pre-catching was set to zero.

For daytime, before noon was set to zero.

For sex, males were set to zero.

Table S3: Context 2 – Field. Top-ranked models from the linear mixed effects models and generalized linear mixed models analysing the effect of GPS transmitter attachment. Parameters explaining the response variables maintenance behaviour, dorsal feather preening, locomotion, foraging, social interactions (including initiated and received affiliative and agonistic behaviours) and CM are given. The individual identity was fitted as random factor. ∆AICc – differences of the second order Akaike information criterion between the best model and the other top-ranked models, logLik – log-likelihood.

Response variable	Model	∆AICc	logLik	Akaike weight
1) Behavioural categories				
Maintenance behaviour	Phase	0.00	-297.697	0.800
Dorsal feather preening	Phase	0.00	1189.778	0.815
Locomotion	Phase	0.00	164.127	0.859
Foraging	Phase	0.00	-189.181	0.814
Initiated affiliative behaviour	Phase+Experimental group+Phase*Experimental group	0.00	-22.919	0.963
Received affiliative behaviour	Phase+Experimental group+Phase*Experimental group	0.00	16.083	0.874
Received agonistic behaviour	Phase	0.00	556.925	0.784
2) Physiological parameter				
CM	Phase+Experimental group+Phase*Experimental group	0.00	-3230.637	1.000

Table S4: Context 2 – Field. Model-averaged coefficients of final models. Shown are the coefficients including adjusted standard errors (SE), lower and upper confidence intervals (CI) as well as the relative importance of the top-ranked models.

Response variable	**Coefficients**	**Estimate**	**Adjusted SE**	**CI lower limit (2.5%)**	**CI upper limit (97.5%)**	**Relative importance**
1) Behavioural categories						
Maintenance behaviour	Intercept	0.671	0.039	0.492	0.627	
	Phase 3	-0.157	0.049	-0.153	0017	1
	Phase 4	-0.339	0.048	-0.292	-0.113	1
	Phase 5	-0.141	0.058	-0.119	0.115	1
Dorsal feather preening	Intercept	0.981	0.012	0.914	0.982	
	Phase 3	-0.025	0.014	-0.039	0.012	1
	Phase 4	-0.004	0.017	-0.002	0.063	1
	Phase 5	0.013	0.017	0.006	0.076	1
Locomotion	Intercept	0.641	0.040	0.564	0.720	
	Phase 3	0.074	0.036	0.028	0.168	1
	Phase 4	0.279	0.051	0.234	0.441	1
	Phase 5	0.187	0.048	0.073	0.272	1
Foraging	Intercept	0.439	0.045	0.428	0.609	
	Phase 3	0.193	0.045	0.018	0.194	1
	Phase 4	0.492	0.072	0.265	0.550	1
	Phase 5	0.246	0.059	0.032	0.282	1
Initiated affiliative behaviour	Intercept	0.900	0.067	0.768	1.031	
	Logger group	-0.105	0.090	-0.282	0.072	1
	Control group	0.006	0.094	-0.179	0.190	1
	Phase 3	-0.131	0.057	-0.242	-0.020	1
	Phase 4	-0.274	0.061	-0.394	-0.154	1
	Phase 5	-0.144	0.067	-0.276	-0.013	1
	Logger group*Phase 3	0.232	0.081	0.073	0.391	1
	Control group*Phase 3	-0.074	0.077	-0.226	0.077	1
	Logger group*Phase 4	0.174	0.091	-0.004	0.353	1
	Control group*Phase 4	0.128	0.089	-0.047	0.303	1
	Logger group*Phase 5	0.012	0.094	-0.172	0.197	1
	Control group*Phase 5	-0.008	0.095	-0.194	0.179	1
Received affiliative behaviour	Intercept	0.897	0.062	0.774	1.019	
	Logger group	-0.071	0.084	-0.235	0.094	1

	Control group	0.023	0.087	-0.148	0.195	1
	Phase 3	-0.164	0.053	-0.268	-0.060	1
	Phase 4	-0.353	0.055	-0.461	-0.245	1
	Phase 5	-0.183	0.062	-0.305	-0.061	1
	Logger group*Phase 3	0.249	0.077	0.099	0.400	1
	Control group*Phase 3	0.059	0.076	-0.091	0.209	1
	Logger group*Phase 4	0.284	0.086	0.116	0.452	1
	Control group*Phase 4	0.188	0.085	0.023	0.354	1
	Logger group*Phase 5	0.151	0.092	-0.029	0.331	1
	Control group*Phase 5	-0.020	0.090	-0.197	0.157	1
Received agonistic behaviour	Intercept	0.886	0.031	0.825	0.948	
	Phase 3	0.060	0.031	0.000	0.120	1
	Phase 4	0.069	0.037	-0.005	0.142	1
	Phase 5	-0.010	0.036	-0.080	0.060	1
2) Physiological parameter						
CM	Intercept	104.266	10.117	84.437	124.094	
	Control group	-30.517	14.379	-58.699	-2.335	1
	Logger group	-17.682	14.353	-45.813	10.449	1
	Phase 2	-31.243	26.293	-82.776	20.291	1
	Phase 3	-33.004	11.749	-56.031	-9.977	1
	Phase 4	-62.831	12.121	-86.588	-39.074	1
	Phase 5	-29.239	12.121	-53.379	-5.098	1
	Control group*Phase 2	-16.238	68.329	-150.161	117.684	1
	Logger group*Phase 2	0.533	41.379	-80.568	81.635	1
	Control group*Phase 3	24.244	16.708	-8.503	56.990	1
	Logger group*Phase 3	4.711	16.255	-27.148	36.570	1
	Control group*Phase 4	29.116	17.264	-4.721	62.953	1
	Logger group*Phase 4	40.769	17.648	6.180	75.358	1
	Control group*Phase 5	10.356	17.861	-24.651	45.364	1
	Logger group*Phase 5	11.563	17.876	-23.474	46.600	1

For experimental group, handling group was set to zero.

For phase, phase 1 was set to zero.

CHAPTER IV

RESEARCH ARTICLE

Space use and site fidelity in the endangered Northern Bald Ibis (*Geronticus eremita*): Effects of age, season and sex

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In resubmission to Bird Conservation International

Picture credit: Roobert Bayer

Abstract

Understanding space use of endangered species is critical for conservation planning and management. The advances in technology and data analysis allow us to collect data with unprecedented quality and inform us about the movements and habitat use of individuals and groups. With only about 700 individuals left in the wild, the Northern Bald Ibis *Geronticus eremita* is currently categorized as endangered. However, little is known about the movements of this avian species in relation to breeding and individual differences. Using GPS transmitters we studied the movements of 32 Northern Bald Ibis from a semi-wild free-flying colony at the Konrad Lorenz Research Center in Austria during 1 to 4 years per individual. We investigated how sex, age class, breeding and non-breeding season affect space use and site fidelity. We found that individuals consistently showed high site fidelity, adults more than juveniles, and space use was highly overlapping between individuals and over successive years. When moving between different areas birds used consistent flyways thereby avoiding direct routes over mountainous areas. Adults had more expansive space use during the breeding season as compared to the non-breeding season, while juveniles only showed a slight decrease during the non-breeding season. We found no sex differences regarding space use or site fidelity. Our results lead to a better understanding of how Northern Bald Ibis move through their environment and how they use foraging areas, roosting sites and space in general that in turn can help to inform conservation management of extant colonies and reintroduction programmes for new colonies.

Keywords: space use, site fidelity, age class, reproductive season, Northern Bald Ibis

Introduction

Movement patterns and space use of individuals and populations are closely linked with survival and fitness and are therefore a key topic in conservation (Berger-Tal *et al.* 2011). Technologies, such as GPS transmitters, have greatly improved wildlife monitoring and generate valuable information for management decisions that involve patterns of habitat use (Berger-Tal & Lahoz-Monfort 2018). Distribution patterns, abundance and biodiversity are affected by landscape characteristics (Saïd & Servanty 2005) and fragmentation (Fritz *et al.* 2003). Human pressures on the environment (i.e. land cover change, infrastructure, access into natural areas), including actions that inhibit road-crossing movements (Ascensao *et al.* 2017; Laurance *et al.* 2004) or human sea traffic that affects marine mammals' movement patterns (Rutz *et al.* 2020; Timmel *et al.* 2008), highlight the need to implement conservation measures (Rutz *et al.* 2020; Venter *et al.* 2016). About forty percent of the world's bird populations are already in decline, mostly because of agriculture, logging, hunting, invasive species and climate change (BirdLife International 2018b; Rosenberg *et al.* 2019), emphasizing the need to generate new or improve existing conservation management strategies. Thus, knowledge about individuals' home ranges and individual variation in habitat use, as well as information about where foraging activities, mating and offspring rearing occur are relevant to better manage threatened populations and species.

Individual space use is affected by abiotic factors, such as habitat quality (Betts *et al.* 2008; Bjørneraas *et al.* 2012) or season (King *et al.* 2016; Ofstad *et al.* 2019), and individual factors, such as age (Šklíba *et al.* 2016), sex (Aronsson *et al.* 2016; Ofstad *et al.* 2019), or reproductive status (Aronsson *et al.* 2016; Wikenros *et al.* 2016). In Black-Throated Blue Warblers *Dendroica caerulescens*, older individuals tend to occupy high quality habitats and leave lower quality habitats to younger individuals (Holmes *et al.* 1996). Such studies underscore the significance of age in space use patterns. In Moose *Alces alces*, males showed greater space use than females during summer (calve rearing period) but not winter (Ofstad *et al.* 2019). Similarly, Eurasian Lynx *Lynx lynx* had sex-specific and seasonal space use: males reduced their space use during mating season and were near females, while females reduced their space use during post-partum when constrained by the impeded movement of offspring (Aronsson *et al.* 2016).

Individuals often return to specific areas within their home range, such as profitable foraging areas or water holes. In Elks *Cervus elaphus*, for example, individuals regularly return to high value foraging patches (Seidel & Boyce 2015), while in Forest Elephants *Elephas maximus borneensis*, individuals return frequently to foraging areas where they had spent more time in the past (English *et al.* 2014). Site fidelity has been found to be dependent on various factors, such as habitat variability (Switzer 1993) and habitat quality (Switzer 1997), but also age (Pyle *et al.* 2001; Switzer 1997), sex (Beheler *et al.* 2003) or breeding success (Shields 1984). Site fidelity is expected to be favoured in predictable habitats, while increasing unpredictability is expected to lead to an increase in movement to more ‘attractive’ habitats when habitat quality is unequal among available habitats (Switzer 1993). In particular, species showing a high degree of site fidelity are more likely to face population decline due to habitat degradation and loss (Warkentin & Hernández 1996). In forest passerines, site fidelity increased with age in declining species that use shrubland during migration (Schlossberg 2009). Different levels of site fidelity would require different conservation strategies (Schlossberg & King 2007; Theobald *et al.* 2000), demanding in some cases tailored conservation approaches at the species or even population level.

The colonial Northern Bald Ibis *Geronticus eremita* is an endangered avian species (BirdLife International 2020), with only about 700 individuals left in the wild in the Souss Massa National Park in Morocco (Oubrou & Bekkay 2018) and additionally about 230 individuals in semi-captivity in the Birecik Breeding Centre in Turkey with the last wild birds in Syria thought now to be locally extinct (Böhm *et al.* 2020). The main factors leading to the disappearance from its former range are habitat destruction, persecution and agricultural pesticides (Collar *et al.* 1985; Hirsch 1976, 1979). Due to reintroduction projects across Europe, the Northern Bald Ibis is also present in Spain, Austria and Germany (Quevedo *et al.* 2004; Unsöld & Fritz 2014); but these populations are not self-sustaining yet and rely on management. Despite occupying different environments to that of the remaining wild birds in Morocco and elsewhere, valuable lessons can be learned from tracking a semi-wild but free-flying colony, as all birds are individually marked and long-term data collection is possible allowing conclusions at individual and group level. The birds are seasonally monogamous, and both older individuals (Sorato & Kotrschal 2006) and males (Böhm & Pegoraro 2011) have higher social dominance rank compared to younger individuals and/or females. Northern Bald Ibis perform movements on different scales, i.e. migration (Syrian population; Lindsell *et al.* 2009; Serra *et al.* 2015) and dispersal (Böhm *et al.* 2020; Serra *et al.* 2015) on a large scale, and diurnal movement patterns when they forage in different sized subgroups during the day and roost together at night on a smaller scale (Böhm & Pegoraro 2011; Smith *et al.* 2008). Younger birds are more likely to disperse than older birds (Böhm *et al.* 2020) and younger individuals in the extinct migratory eastern population in Syria (Böhm & Bowden 2016) seemed to have a different overwintering area than adults (Lindsell *et al.* 2009). Only few data about movement and habitat use exist from extant or recently extinct populations and these data indicate that Northern Bald Ibis are rather consistent in habitat use (Serra *et al.* 2008). However, to protect the remaining colonies and aid the reintroduction of further populations, a better knowledge about their movement behaviour is needed.

In this study, we investigate space use of individually marked and free-flying Northern Bald Ibis. Specifically, we measure (1) the area used, (2) the consistency of space use over time, (3) the consistency of flyways between areas, (4) site fidelity to locations of interest, and (5) factors (sex, age class, biological relevant season) that may influence space use and site fidelity. We tested the prediction that Northern Bald Ibis will differ in space use between age class (i.e. juveniles and adults) and season (i.e. breeding and non-breeding season), but still show large overlap between individuals and years. We expect a consistent use of particular sites over time and consequently a consistent use of flyways between areas. Specifically, we predict (1) no sex differences in space use and site fidelity due to relatively similar behavioural patterns in both females and males (Sorato & Kotrschal 2006), (2) restricted space use by adults compared to juveniles during the breeding season compared to the non-breeding season due to parental care in breeding individuals (Zurell *et al.* 2018) and juvenile dispersal during autumn (Böhm *et al.* 2020), and (3) consistent high site fidelity to locations of interest (e.g. foraging habitats) due to rather predictable habitats, and higher site fidelity in adults than juveniles as site fidelity increases with age (Switzer 1993).

Methods

Field site and study animals

This study was conducted at the Konrad Lorenz Research Center in Grünau im Almtal (Upper Austria, 47°48’E, 13°56’N, Figure 1). The colony at the research center was the first semi-wild free-living colony north of the Alps in 400 years (Kotrschal 1999). The year-round free-flying Northern Bald Ibis colony has access to an open aviary at the local Herzog-von-Cumberland game park (approximately 20 x 15 x 7 m [L x W x H]). The only exception to this free-flight access was in 2013, when all birds were locked inside the aviary from 2 to 12 July 2013 as part of an experiment (Puehringer-Sturmayr *et al.* 2020). During the post-fledging period, birds forage in the Almtal valley and return to the aviary for roosting and breeding. During summer and early autumn (approximately from July to September), the birds usually fly to the vicinity of Molln (a village 25 km linear distance from the research center) and return late autumn to Grünau im Almtal when decreasing temperature constrains food availability (Frigerio & Gegendorfer 2013). All birds are individually marked with combinations of coloured leg rings and a metal leg ring with a unique alpha-numerical code from the German or Austrian ornithological station. During the winter and breeding season, birds are food supplemented (hash made from 1-day-old chicks and beef heart, mixed with soaked dry dog food and insects) at the meadow in front of the research center or in the aviary. During winter (November to February), food is available ad libitum and all individuals are able to feed to saturation; during the breeding season (March to June), the supplemental feeding is made available twice per day (0800, 1500) and birds regularly forage on the nearby foraging grounds. The birds are not supplemented with food during summer and autumn. At the time of data collection, the colony had the following group sizes: $N_{2013} = 70$, $N_{2014} = 53$, $N_{2015} = 41$, $N_{2016} = 51$ birds. On average, 17 ± 8 (mean ± SD) chicks fledge each year. In 2013, a population increase was recorded because of the exceptionally large number of fledged chicks (27 individuals). The population decreased between 2013 and 2014 due to juvenile dispersal (Böhm *et al.* 2020) and higher predation by birds of prey (Kotrschal *et al.* 1992).

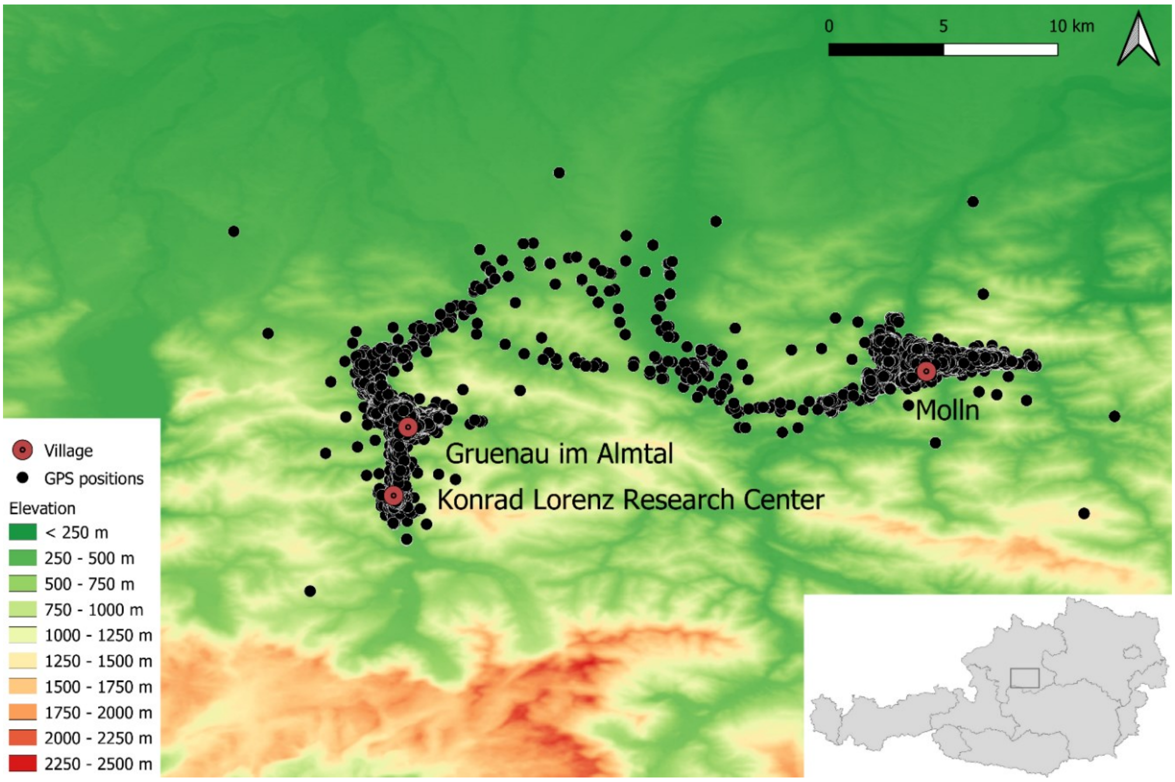

Figure 1. Study area in the northern Austrian Alps. The GPS positions of 32 Northern Bald Ibis are shown (black dots). On the bottom right a map of Austria is shown with a rectangle indicating the main map. Background digital elevation model (DEM) was derived from oe3d in spatial resolution 1 arc second (approximately 20-30 m, http://www.oe3d.at/).

Study design

From 2013 to 2016 during the breeding and non-breeding season a total of 32 focal individuals (17 males and 15 females; sex of the individuals was determined genetically, from blood samples after polymerase chain reaction done at Laboklin GmbH & Co.KG; for details on individuals see Table 1) were equipped with backpack-mounted GPS transmitters using a harness (as described in Lindsell *et al.* 2009; GPS transmitters were removed during winter from November to March). Out of those, 12 birds were GPS-tagged over several successive years (i.e. between 2 and 4 years, Table 1). Focal individuals were classified into two age classes according to Böhm & Pegoraro (2011): (1) juveniles, i.e. immature and subadult birds (first to third year after hatching; N_{2013}=5 [2 males and 3 females], N_{2014}=0, N_{2015}=7 [3 males and 4 females], N_{2016}=2 [2 females]), and (2) adults (from fourth year on; N_{2013}=6 [4 males and 2 females], N_{2014}=4 [1 male and 3 females], N_{2015}=10 [5 males and 5 females], N_{2016}=14 [9 males and 5 females]). The potential lifespan for the Northern Bald Ibis in captivity is 30 to 40 years (Böhm & Pegoraro 2011). The start and end of the breeding season was determined separately for each breeding individual depending on the individual variation in the start of egg-laying. Breeding season started with the first laid egg (laid between 6 February and 27 March) and ended with the last fledged chick (fledged between 8 June and 9 July) in a single clutch for breeding individuals (average number of days breeding = 74 days). To be able to compare the spatial use of breeders and non-breeders during the breeding season, we defined this period for the non-breeders as the time from the first laid egg till the last fledged chick of the colony. Non-breeding season comprised summer and autumn (i.e. period in which no supplemental food was provided), but not the wintering season.

Table 1. Focal individuals. Name, sex (m=male, f=female), year of hatching, age class, year/s with GPS data (2013 – 2016), number of GPS positions (*n* fixes), space use size of the 95 % utilisation distribution (95 % UD) and number of days the individuals were tagged are indicated.

Individual	Sex	Year of hatching	Age class	Year of deployment	*n* fixes	95 % UD [km²]	Days tagged
Agatha	f	2011	juvenile	2013	1234	0.36	86
Aleppo	f	2006	adult	2014	2289	0.57	201
				2015	2792	0.36	173
				2016	3955	0.21	217
Azzurro	m	2015	juvenile	2015	2772	0.18	171
Balu	m	2010	adult	2015	2472	0.74	175
Cian	m	2008	adult	2013	1502	0.17	84
				2016	2868	0.97	190
Diabolo	f	2014	juvenile	2016	2684	0.47	150
Ferdinand	m	2013	juvenile	2013	1378	0.45	86
Gina	f	2013	juvenile	2013	749	-	64
Goran	f	2005	adult	2013	1193	0.07	66
Hermine	f	2012	adult	2015	3136	0.72	211
				2016	1021	0.39	48
Hilda	m	2009	adult	2013	1098	0.22	86
				2016	159	0.81	25
Hombre	m	2002	adult	2015	3202	0.85	205
Jarmusch	m	2005	adult	2013	1853	0.12	110
Khan	m	2013	adult	2016	3102	0.81	207
Kleopatra	f	2013	juvenile	2015	2998	0.72	201
			adult	2016	3812	0.37	210

Loki	f	2006	adult	2014	2684	0.63	238
				2015	3363	0.56	214
Lukas	m	2012	juvenile	2013	1403	0.45	86
			adult	2016	2940	0.71	196
Othello	m	1999	adult	2015	3229	0.43	191
				2016	3096	0.28	215
Ozzy	m	2010	adult	2016	3439	0.79	208
Rob	m	2010	adult	2013	1533	0.16	86
Rosa	f	2013	juvenile	2013	1448	0.29	85
Sandro	f	2015	juvenile	2015	2869	0.24	171
Saphira	f	2015	juvenile	2015	2804	0.19	171
Schreckse	f	2008	adult	2015	2502	1.19	180
				2016	3657	0.42	202
Sequoia	f	2009	adult	2013	1523	0.14	88
				2014	2270	0.67	189
				2015	3780	0.83	216
				2016	3611	0.54	191
Shannara	m	2007	adult	2014	2201	0.52	148
				2015	3826	0.59	215
				2016	322	0.78	44
Simba	m	2015	juvenile	2015	2623	0.27	213
Simon	m	2006	adult	2015	3803	0.78	215
				2016	3023	0.68	217
Sino	f	2014	juvenile	2015	3054	0.21	171
Smirne	m	2015	juvenile	2015	2082	0.18	156
Taska	f	2014	juvenile	2016	3451	0.52	201
Tiffi	m	2011	adult	2016	2956	1.00	196

Measuring space-use patterns with GPS transmitters

GPS data were collected from April 2013 to October 2016 during the breeding and non-breeding season. Focal individuals (with body mass ranging from 1020 g to 1500 g at the start of the study) were equipped with GPS transmitters (Ecotone® Telemetry, Sopot, Poland; http://ecotone-telemetry.com/en) that were all solar powered and data were downloaded via a UHF link (model: HARIER, weight: 20 g) or using the GSM network (model: DUCK-4 Solar, weight: 28 g; model: SAKER M, weight: 19 g). Fitting the loggers on the birds lasted on average 18.6 ± 4.7 minutes (mean ± SD) per bird. The loggers constituted less than 3 % of the body mass of the smallest bird (Phillips *et al.* 2003). Although GPS transmitters are suspected to cause unilateral corneal opacity in two other Northern Bald Ibis populations (Fritz *et al.* 2020), we did not observe such a physiological effect or any physical damage, such as abrasion or feather loss, in our study population. We also could not find effects of the GPS transmitters on behaviour or body weight in Northern Bald Ibis, but we found an increase in the excretion of corticosterone metabolites about a month after deployment (Puehringer-Sturmayr *et al.* 2020).

We monitored complete daily movements between 0400 and 1900. The average tracking interval between GPS fixes was 62.46 ± 22.71 minutes (mean ± SD). In case of low battery status during bad weather conditions, we increased the time between two fixes to enable a quicker recharging of the batteries.

Data analysis

Calculations of space use and site fidelity to locations of interest were treated separately over successive years, since GPS transmitters were removed during winter. As the sampling rate differed between individuals, we reduced the GPS data points to an hourly sampling rate for further analyses (i.e. only the first data point of each hour was included in the final data set). All analyses were conducted with the program R version 4.0.2 (R Core Team 2020).

Estimation of space use

We used the home range bootstrap method to calculate the number of locations required to provide robust estimates of space use. This method allowed us to assess from which focal individuals we had collected sufficient GPS data points to include in the analyses to calculate accurate estimations of space use. To estimate the space use for each individual in each year and season, we calculated the utilisation distribution (UD). A UD is a probability density representing an animal's relative frequency of occurrence in space and time. Thus, strictly speaking we did not estimate the entire home range (see definition of Burt 1943), instead we were interested in the birds' occurrence distribution during the tracking period. Subsequently, area size was calculated in km² for the 95 % space use per individual, season and study year.

The home range bootstrap function (Kranstauber *et al.* 2020) was used to calculate and plot the area size of the minimum convex polygon (MCP, a traditional home range estimation method compared to the dBBMM used to calculate the UD; the MCP is meanwhile rarely used to estimate home ranges, but rather to describe the distribution of locations required for home range estimation; Nilsen *et al.* 2008) of the trajectories per season using an increasing number of coordinates that first leads to an increase in areas size until it reaches a plateau. This plateau indicates whether an individual's home range is stable, which marks the minimum number of GPS points required to realistically represent the animal's space use that we identified through visual inspection of the plot. Thus, individuals with fewer than 90 GPS positions during the breeding season (Figure S1, pertained the data collected during the breeding season of 1 individual) and individuals with fewer than 800 GPS positions during the non-breeding season (Figure S2, pertained the data collected during the non-breeding season of 3 individuals) were not included in the analyses. Consequently, the final data set included 31 focal individuals (in total 17 males and 14 females; 13 juveniles – 5 males and 8 females, 20 adults – 13 males and 7 females; the number of GPS-tagged juveniles and adults does not add up to 31 individuals because 2 individuals were allocated to different age classes, depending on their age in the respective year), which was used for all further analyses regarding space use and site fidelity.

We calculated the utilisation distribution (UD) with dynamic Brownian bridge movement models (dBBMM; Kranstauber *et al.* 2012) using the "move" package (Kranstauber *et al.* 2020). Space use was defined as the area within the 95 % contour of the estimated UD. The dBBMM is a method incorporating the detection of change in movement patterns (e.g. movement versus rest, foraging versus moving between sites) along an animal's trajectory by using behavioural change point analysis (Kranstauber *et al.* 2012). To account for changes in behaviour, the dBBMM allows the Brownian motion variance (i.e. detection of changes in turning angles, speed, step length) to vary along an animal's trajectory for a pre-specified subset of *n* locations (windows sliding along an animal's trajectory). Following the recommendations of Kranstauber *et al.* (2012) to select a margin size of 9-11 locations and a window size of around 30 locations, we selected the following parameters for the dBBMM to account for potential variations in movement patterns between days, as Northern Bald Ibis are rather consistent in habitat use: (1) window size (i.e. size of the sliding window along an animal's trajectory) was chosen based on the temporal resolution of each trajectory and was set to 31 GPS positions (i.e. with a maximum number of 15 GPS positions received per day for an individual this would translate into a window length of 2 days) and (2) margin size for the behavioural change point analysis (i.e. margins at the start and end within each window in which no changes of behavioural state can occur) was set to 11 GPS positions (11 hours). Average telemetry error associated with each location was determined by the transmitter manufacturer as ± 20 m. Focal individuals had varying numbers of GPS positions, due to different tagging dates and sampling rates, variation in battery recharging and/or possible GPS transmitter failures. Consequently segments with time gaps larger than 960 minutes were removed (i.e. when two consecutive GPS positions had a large time gap, those two GPS positions were not included in the calculation of the dBBMM) to avoid uncertainties of where the animal may have been during the missing data. For visualisation, we exported UDs as shapefiles and overlaid them with a digital elevation model (derived from oe3d, spatial resolution approximately 20-30 m, http://www.oe3d.at/) of the study area in QGIS (QGIS Development Team 2019).

Step-selection function

We used a step selection function (SSF, Fortin *et al.* 2005) using the amt package (Signer *et al.* 2019) to investigate whether Northern Bald Ibis use consistent flyways along valleys between areas or direct routes over mountainous areas. The environmental covariate (i.e. elevation) was derived from the ASTER Global Digital Elevation Model (spatial resolution 1 arc second, 30 m) using the environmental-data automated track annotation (Env-DATA) System of Movebank (Figure S3, Dodge *et al.* 2013).

GPS points within a trajectory were converted to steps including step lengths and relative turning angles. For each observed step (movement between two consecutive locations), we created 10 random steps (as it was suggested that a low number of random steps is sufficient to calculate availability of locations, Thurfjell *et al.* 2014). Each observed step with its corresponding random step was assigned to a unique step ID. From this step representation, used locations can then be compared to available locations (Thurfjell *et al.* 2014). We implemented a two-step approach provided by the TwoStepCLogit package (Ts.estim function, Craiu *et al.* 2016) to obtain population level selection patterns and relate individual β coefficients to animal-specific characteristics (i.e. sex, age class). We used a mixed-effects conditional logistic regression with the binary response of used and available locations as response variable. Subject identity was set as the cluster and the unique step ID as the strata. The model was fit with additive fixed- and random-effects of the environmental covariate elevation across clusters. The mixed-effects conditional logistic regression was fitted to each animal (subject ID as cluster). Afterwards, (1) coefficients and standard errors were summarized across all individuals to infer population level selection patterns, and (2) to infer sex- and age class-specific effects, β coefficients of each individual were extracted and the estimates treated as data to relate coefficients to animal-specific characteristics (see 'Statistical modelling' section for details on the animal-specific characteristics model).

Site fidelity to locations of interest

To identify areas that were frequently visited (e.g. nesting, roosting and foraging sites) by the 31 focal individuals, we used the package "recurse" (Bracis *et al.* 2018). Highly visited sites were identified and we extracted the top 5 % (calculated from the number of revisitations) of the most revisited locations per individual. Because the focal individuals frequented a high number of different locations in the study areas (up to 192 highly visited locations during the breeding season and 179 highly visited locations during the non-breeding season), only the top 5 % were extracted to analyse locations with the highest frequency of revisitations, which reflects site fidelity (i.e. few highly visited sites would imply relatively high site fidelity compared to many highly visited sites). For further analysis the number of top 5 % locations was counted per individual.

The recurse method creates a radius moving along an animal's trajectory. Each time the trajectory enters and exits the radius, it is counted as a revisitation. Areas of high usage are identified by the number of revisitations. Each individual was separately analysed for each study year (2013-2016) and season (i.e. breeding and non-breeding season). Constraints such as the accuracy of the GPS transmitters used in this study (± 20 m) and an hourly sampling rate were taken into consideration when selecting the radius size of 100 m.

Statistical modelling

We assessed which factors influence the following response variables: (1) area size (i.e. 95 % space use), (2) individual β coefficients of the SSF models, and (3) site fidelity (i.e. number of top 5 % highly visited locations). To avoid collinear factors in the model, reproductive status was not included as a fixed factor in the analyses, as most adult focal individuals were breeders and juveniles do not breed. Prior to fitting the models, the predictor 'number of GPS positions' was z-transformed to get an easier interpretable model (Schielzeth 2010) and ease model convergence.

To assess the influence of sex, season (i.e. breeding and non-breeding season), and age class (i.e. juveniles and adults; all three variables included as fixed effects) on area size, we used a Generalized Linear Mixed Model (Baayen 2008) with a gamma error distribution, log link function and the optimizer 'bobyqa'. We also included the interaction between season and age class (as we anticipated seasonal differences between juveniles and adults) as well as number of GPS positions (to control for potential effects of number of GPS positions) as further fixed effects. As random effects, we included subject identities and study year. The reason for including these random effects was that some individuals were observed more than once between study years and to control for different conditions (e.g. environment-related) between years.

To relate SSF β coefficient estimates (calculated for the environmental covariate elevation) from each individual to animal-specific characteristics, we performed a Multiple Regression including sex and age class as predictors.

To analyse the influence of sex, season (i.e. breeding and non-breeding season), and age class (i.e. juveniles and adults) on site fidelity (i.e. number of top 5 % highly visited locations), we used a Generalized Linear Mixed Model (Baayen 2008) with a negative binomial error distribution (due to overdispersion of the poisson model: overdispersion $\text{parameter}_{\text{poisson}}$ = 24.27, overdispersion $\text{parameter}_{\text{negative binomial}}$ = 1.20) with these three variables and the interaction between season and age class included as fixed effects into the model. As random effects, we included subject identities and study year.

An information theoretic approach (Burnham & Anderson 2002) was used to calculate all possible candidate models and select the best models. The top models were ranked according to their AICc values (second order form of Akaike's information criterion to account for small sample sizes; Hurvich & Tsai 1989) and we selected the models with a ∆AICc ≤ 6 (Harrison *et al.* 2018). The relative importance of each predictor is calculated from the Akaike weight by summing the weights of the top-ranked models in which the predictor occurs. Thus, relative importance informs about the degree of importance of the predictor. The top-ranked models were averaged in order to create model-averaged coefficients following Burnham & Anderson (2002).

Statistical modelling was conducted using the functions lm and glmer of the package 'lme4' (Bates *et al.* 2015) and the information theoretic approach was done with the package 'MuMIn' (Barton 2020).

Results

Space use

In total, we recorded 113,643 GPS positions between April 2013 and October 2016 (minimum and maximum numbers of GPS positions per bird and season: breeding season – min = 92, max = 1134; non-breeding season – min = 1098, max = 3075) from the final sample size of 31 individuals. The space use utilisation distribution (UD) for each individual comprised on average 0.56 ± 0.44 km² (95 % UD, mean ± SD, range = 0.005 to 1.92 km²). Space use was on average greater during the breeding season (mean ± SD = 0.91 ± 0.48 km²) than during the non-breeding season (mean ± SD = 0.31 ± 0.14 km²). The UD overlap between individuals and years was extremely high (Figure 2).

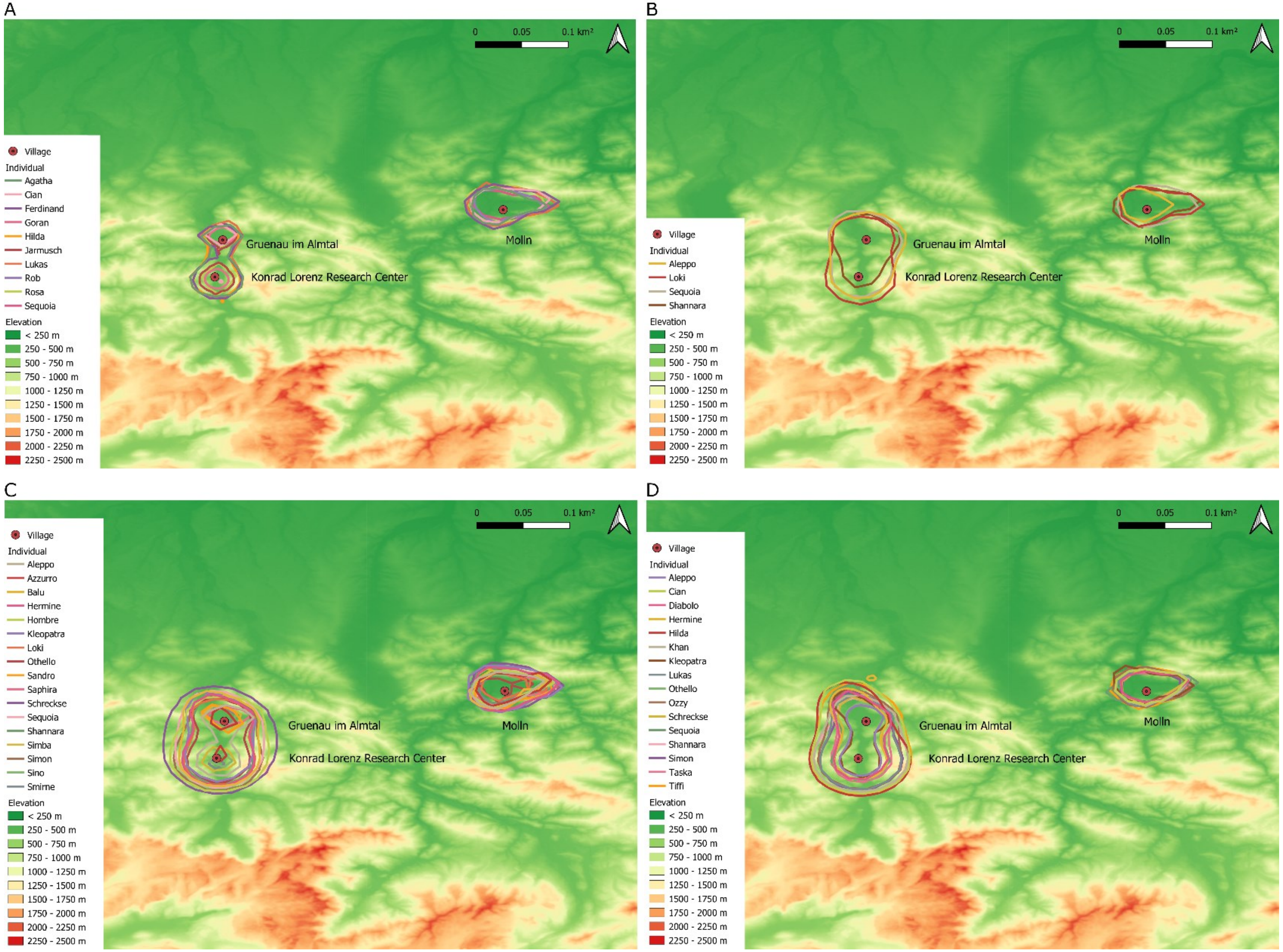

Figure 2. Space use polygons for the 95 % utilisation distribution are shown with different colours for different individuals. Data collected in (A) 2013 (N=10), (B) 2014 (N=4), (C) 2015 (N=17) and (D) 2016 (N=16). Background digital elevation model (DEM) was derived from oe3d in spatial resolution 1 arc second (approximately 20-30 m, http://www.oe3d.at/).

Step selection

At the population level, birds consistently used flyways along valleys rather than direct routes over mountainous areas when moving between areas (β = -0.023, SE = 0.001, relative selection strength for low elevations [RSS, exp(β)]=0.98, Avgar *et al.* 2017, Figure S4). Sex and age class did not improve model fit over the null model (assessed by AICc) indicating that these factors had no impact on locations used related to elevation (Table 2).

Table 2. Top-ranked models with a ΔAICc ≤ 6 for SSF β coefficient estimates in relation to animal-specific characteristics. Given are the predictors influencing the β coefficient estimates as well as degrees of freedom (Df), log-likelihood (logLik), delta AICc (differences of the second order Akaike information criterion between the best model and the other top-ranked models) and Akaike weight.

Predictors	Df	logLik	ΔAICc	weight
age class	3	162.482	0.00	0.717
age class, sex	4	162.532	2.28	0.229
Intercept only	2	158.752	5.18	0.054

Site fidelity to locations of interest

Across different years, Northern Bald Ibis showed a consistent use of particular locations with some specific foraging grounds having a higher re-use between years than others. The more frequently visited sites were located on meadows along valleys in both study areas Grünau im Almtal and Molln (Figure 3). Furthermore, the highly visited sites appear to be clumped in some areas. One of those sites in Grünau im Almtal is used as a nest site (i.e. aviary in the game park). The other locations are foraging and roost sites. The nest site and nearby foraging areas around the Almtal valley (i.e. Grünau im Almtal) were especially frequented during the breeding season and late non-breeding season (i.e. autumn, season shortly before wintering season). In contrast, foraging areas around Molln were frequented during the non-breeding season.

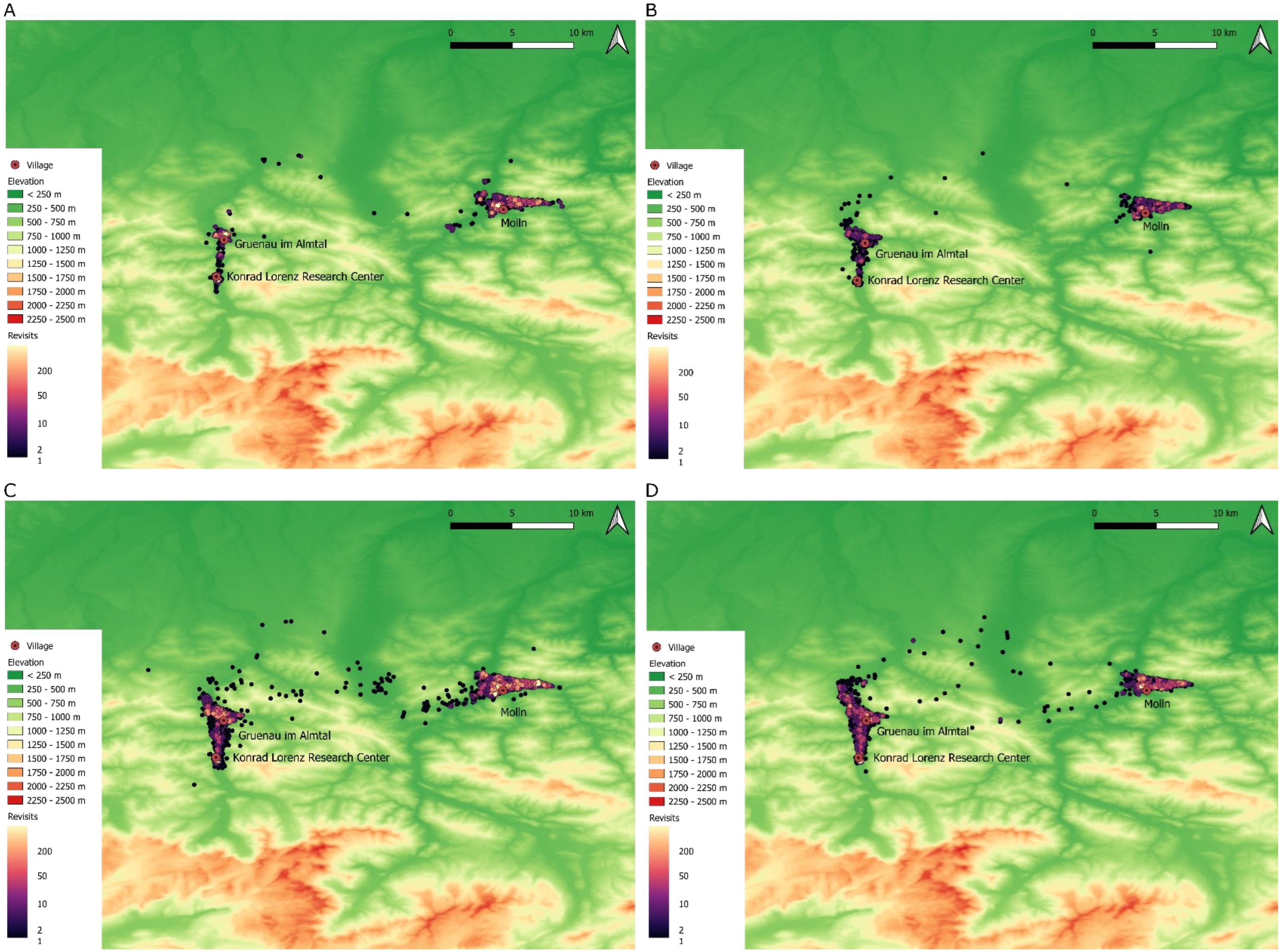

Figure 3. Movement data in the breeding and foraging habitats Grünau im Almtal and Molln, Upper Austria, Austria. The number of revisitations to a location is shown on a logarithmic scale from black (low) to yellow (high), with several areas of concentrated visits apparent. Data collected in (A) 2013 (N=11), (B) 2014 (N=4), (C) 2015 (N=17) and (D) 2016 (N=16). Background digital elevation model (DEM) was derived from oe3d in spatial resolution 1 arc second (approximately 20-30 m, http://www.oe3d.at/).

Factors influencing space use and site fidelity

Splitting up the data per individual, season and study year resulted in 76 space use estimations (95 % UD) from 31 individuals. The interaction between age class and season best explained the size of the 95 % UD of Northern Bald Ibis (Table 4 and 5). Adult and juvenile space use was more expansive during the breeding season as compared to the non-breeding season, but this effect was less pronounced for juveniles (Table 3 and 5, Figure S5). Furthermore, juveniles had more restrictive space use than adults during the breeding and non-breeding season (Table 3 and 5). Compared to the interaction term age class x season, the relative importance of sex and number of GPS positions was very low (Table 5); thus, these factors had a less important influence on the size of the 95 % UD.

The main effects season and age class best explained site fidelity (Table 4 and 5). Individuals had a higher site fidelity during the non-breeding season than the breeding season (Figure S6) and adults showed a higher site fidelity as compared to juveniles (Table 3 and 5, Figure S7). Compared to season and age class, the relative importance of sex and the interaction between age class and season was very low (Table 5).

Discussion

We found a range of factors that affected space use patterns in Northern Bald Ibis. (1) In this study Northern Bald Ibis had a high degree of spatial overlap between different individuals and across successive years, and (2) they used consistent flyways along valleys but avoided direct routes over mountainous areas. (3) Individuals showed a consistent use of particular sites across years. There was an interaction effect between age class and season with (4) adults and juveniles showing more expansive space use during the breeding season than the non-breeding season, but this effect was less pronounced in juveniles. (5) Site fidelity was overall higher during the non-breeding season compared with the breeding season irrespective of individual age, and adults generally had higher site fidelity than juveniles irrespective of the season.

Table 3. Response variables with corresponding predictor variables including their levels, mean and standard deviation of the raw data are shown.

Response variable	Predictors	Levels	Mean	SD
95 % Space use [km²]	Sex	females	0.51	0.39
		males	0.61	0.49
	age class	adults	0.64	0.47
		juveniles	0.32	0.20
	Season	breeding season	0.91	0.48
		non-breeding season	0.31	0.14
	age class x season	adults x breeding season	1.01	0.44
		adults x non-breeding season	0.32	0.16
		juveniles x breeding season	0.38	0.35
		juveniles x non-breeding season	0.29	0.11
Site fidelity (i.e. number of the top 5 % of highly visited locations)	Sex	females	33.11	65.42
		males	20.13	27.06
	age class	adults	21.91	43.43
		juveniles	41.06	65.34
	Season	breeding season	38.50	70.99
		non-breeding season	17.68	22.02
	age class x season	adults x breeding season	30.04	60.04
		adults x non-breeding season	14.84	18.67
		juveniles x breeding season	84.20	111.95
		juveniles x non-breeding season	24.46	28.22

Table 4. Top-ranked models with a ∆AICc ≤ 6 for 95% space use and site fidelity. Given are the predictors influencing the response variables 95 % space use and site fidelity as well as degrees of freedom (Df), log-likelihood (logLik), delta AICc (differences of the second order Akaike information criterion between the best model and the other top-ranked models) and Akaike weight.

Predictors	**Df**	**logLik**	**∆AICc**	**weight**
95% Space use				
age class, season, age class x season	7	-352.140	0.00	0.426
age class, season, number GPS positions, age class x season	8	-351.236	0.69	0.301
age class, season, sex, age class x season	8	-352.138	2.50	0.122
age class, season, sex, number GPS positions, age class x season	9	-351.185	3.17	0.087
season	5	-357.039	5.01	0.035
age class, season	6	-356.041	5.37	0.029
Site fidelity (i.e. number of the top 5 % of highly visited locations)				
age class, season	6	-312.894	0.00	0.359
age class, season, age class x season	7	-312.490	1.62	0.160
age class, season, sex	7	-312.890	2.42	0.107
season	5	-315.374	2.60	0.098
age class	5	-315.389	2.63	0.097
intercept only	4	-317.217	3.99	0.049
age class, season, sex, age class x season	8	-312.482	4.11	0.046
season, sex	6	-315.291	4.79	0.033
age class, sex	6	-315.303	4.82	0.032
sex	5	-316.982	5.82	0.020

Table 5. Model-averaged coefficients for 95% space use and site fidelity. Given are the coefficients with adjusted standard errors, lower and upper confidence intervals, z-value, p-value and relative importance of the top-ranked models.

Predictors [levels]	Estimate	Adjusted SE	CI lower limit (2.5%)	CI upper limit (97.5%)	Relative importance
95% Space use					
Intercept	4.573	0.200	4.181	4.966	
age class [juvenile]	-1.070	0.426	-1.854	-0.362	0.97
season [non-breeding season]	-1.274	0.297	-1.856	-0.692	1.00
age class [juvenile] x season [non-breeding season]	1.075	0.471	0.383	1.913	0.94
number GPS positions	0.078	0.135	-0.095	0.495	0.39
sex [male]	0.006	0.083	-0.323	0.383	0.21
Site fidelity (i.e. number of the top 5 % of highly visited locations)					
Intercept	3.106	0.331	2.369	3.733	
age class [juvenile]	0.725	0.577	0.036	2.685	0.80
season [non-breeding season]	-0.514	0.381	-1.206	0.085	0.80
age class [juvenile] x season [non-breeding season]	-0.136	0.435	-2.255	0.784	0.21
sex [male]	-0.015	0.179	-0.640	0.741	0.24

Our food-supplemented colony of Northern Bald Ibis had comparable space use (on average 89.01 km² from April to October calculated with a minimum convex polygon) to the resident western population in Morocco (74.54 km² on cultivations/recent fallows; Bowden *et al.* 2008), but more restricted space use compared to the migratory eastern relict population (ca. 150.00 km² at the breeding site calculated with a minimum convex polygon and 80.80 km² at the wintering site calculated with a fixed-kernel range estimator; Serra *et al.* 2011, 2013). However, habitat use of the Moroccan population was only estimated for foraging areas by observing and following individuals from colonies and roosts to their foraging grounds and marking the exact position on aerial photos (Bowden *et al.* 2008). Thus, space use for this population may be larger than estimated. The more restricted space use compared to the eastern relict population is probably a consequence of food supplementation. In addition, the surrounding meadows of the Alm Valley and Molln area are rich in food (Markut 2005) with high prey densities during spring and summer and provide abundant freshwater sources as compared to Near East or North African environments. In contrast to the conditions in Austria, the desert habitats also pose stringent costs on reproductive success (Smith *et al.* 2008) and possible restraints on space use and time budgets in the Moroccan population due to water shortages.

Despite excellent flight capacity in Northern Bald Ibis (Portugal *et al.* 2014), our study birds consistently used flyways between study areas along valleys rather than direct routes over mountainous areas. Updrafts are often associated with mountains and are used by large raptors (e.g. Goshawk *Accipiter gentilis*, Golden eagle *Aquila chrysaetos*; Duerr *et al.* 2012), which might increase predation risk along mountainous routes. In addition to consistency of travel routes, we also found a high degree of overlap between space use of single individuals and consistent space use across successive years, indicating high space use stability and site fidelity. Similar patterns of consistent space use by individuals were found in Northern Bald Ibis at an Ethiopian wintering site (Serra *et al.* 2013), in Crested Ibis *Nipponia nippon* (Dongping *et al.* 2003), and in non-breeding ravens *Corvus corax* (Loretto *et al.* 2016).

Individual space use patterns may differ across age (Mlyashimbi *et al.* 2020), sex (Lidgard *et al.* 2020; Mlyashimbi *et al.* 2020), and reproductive status (Robinson *et al.* 2017) or may vary with external factors, such as season (Ofstad *et al.* 2019). Similar to observations in King Rails *Rallus elegans* (Kolts & McRae 2017), we found that adults had more expansive space use during the breeding season than during the non-breeding season. Adults increased their foraging radius during breeding, likely to acquire resources to provision offspring. A similar pattern was found in Bearded Vultures *Gypaetus barbatus* (Krüger *et al.* 2014), though not in White Storks *Ciconia ciconia* (Krüger *et al.* 2014; Zurell *et al.* 2018). Up to 50% of the juveniles in our study population disperse at the end of summer/beginning of autumn and fly north/north-east (e.g. to Germany, Poland, Czech Republic, Latvia, the Netherlands), even though some individuals return during late autumn (Böhm *et al.* 2020), which may explain the minor seasonal differences in juvenile space use. Our data did not reveal sex differences in space use as shown for many other bird species (e.g. Aronsson *et al.* 2016; Johansson *et al.* 2018; Tisell *et al.* 2019). For instance, male King Rails used more space during the non-breeding season than females (Kolts & McRae 2017). Females may adapt their space use according to food availability (Aronsson *et al.* 2016) and spend more time foraging than males

(Lidgard *et al.* 2020) to increase survival and fitness. Those differences seemingly scale with sexual dimorphism (Ruckstuhl & Neuhaus 2007). Northern Bald Ibis, however, are hardly sexually dimorphic (Böhm & Pegoraro 2011), not even in their behaviour (Sorato & Kotrschal 2006). Northern Bald Ibis exhibit bi-parental care, are colonial and spend most of their time in a group (Böhm & Pegoraro 2011), explaining the similar space use patterns we observed in males and females. From a conservation perspective, it is useful to know that males and females in this population tend to occupy the same areas at the same times of year.

Animals regularly return to specific sites, such as foraging grounds, nest sites, roosting sites and watering holes (Bracis *et al.* 2018). Site fidelity reflects stability in patterns of space use (Harris & Leitner 2004). In this study, we found evidence for site fidelity with consistent patterns of use of particular sites, such as foraging sites, across successive years at the population level. This could perhaps be attributed to rather predictable and stable habitats during the times when monitoring occurred. Previous studies showed that site fidelity increases with age (Switzer 1993), which could explain the higher site fidelity in adults as compared to juveniles. Adult breeders may have to trade-off exploiting known resources and exploring new ones, which could result in lower site fidelity during the breeding season because of the need to search for high quality resources. Site fidelity can also entail certain risks, including anthropogenic effects. For instance, predator species of Africa and Eurasia (mammals: e.g. Caracals *Caracal caracal*, Honey Badger *Mellivora capensis*; raptors: e.g. Cape Eagle Owl *Bubo capensis*, Palm Nut Vulture *Gypohierax angolensis*) are highly exposed to poison used to control rodent populations mostly associated with proximity to human habitats (Santangeli *et al.* 2019; Serieys *et al.* 2019). Such site-specific risks of the current population are not known for Northern Bald Ibis, but should be kept in mind for future research, specifically because site fidelity appeared to be strongly associated with the size of the relevant area, and site fidelity increased when the utilised space was smaller. As above with regard to the size of space use, there was no effect of sex on site fidelity, which matches well the lack of anatomical or behavioural sexual dimorphism in Northern Bald Ibis (Böhm & Pegoraro 2011; Sorato & Kotrschal 2006).

Conservation implications

Northern Bald Ibis populations decreased over the last century and many colonies disappeared from most of their former range (Bowden *et al.* 2003). This species seems rather consistent in habitat use and foraging sites (Kirnbauer 2004; Serra *et al.* 2008), indicating that site fidelity may play a major role in selecting foraging habitats. Such lack of adaptive flexibility has also been suggested as a reason for the decline of the species throughout its original distribution range. Our work provides insights into the movement ecology of the Northern Bald Ibis, which broadens our understanding of factors that shape space use and site fidelity patterns in an endangered species. As the extant of space use by the study population was comparable to that of the Moroccan population (last persisting viable wild population), our findings can be relevant for any population in the wild and for the adaption of conservation strategies accordingly.

Here, we show that Northern Bald Ibis are extremely consistent in their patterns of space use for resources such as foraging and roosting, despite the availability of similar areas elsewhere. The seasonal- and age-specific differences in movement and space use patterns point to benefits of implementing age-specific approaches to manage movement and space use. In particular, conservation interventions should be encouraged along migration and dispersal routes, as up to 17% and 31% of annual losses in reintroduced colonies are still accounted for by illegal hunting and electrocution, respectively (Böhm *et al.* 2020; Fritz *et al.* 2017), mainly occurring during long distance movements. Thus, designation of protected areas should also be seasonally based. Furthermore, we show that mountainous routes are avoided, which informs reintroduction projects to rather select migration routes along valleys and, by extension, which habitat characteristics (i.e. migration and dispersal corridors through the mountains should be present) to consider when establishing new colonies. This information can be used to improve the protection of existing habitats, but also to identify new habitats for potential reintroduction. These insights can aid the assessment of different reintroduction strategies, the viability and vulnerability of the population in a particular habitat, and be used to estimate the potential distribution range of this species (e.g. Macdonald *et al.* 2000; Macdonald & Rushton 2003).

Site fidelity could constrain the viability of a population in case of habitat degradation and loss, especially when populations inhabit restricted habitats (Warkentin & Hernández 1996). To counteract population decline associated with high site fidelity, threatened and declining species displaying site fidelity need to be monitored and conservation actions need to be adapted. Particularly their habitats need to be monitored and protected against degradation. Small populations are more vulnerable to extinction compared to large stable populations because of loss of gene flow and variability in environment and population size (Caughley & Gunn 1996). Thus, populations with high site fidelity could face higher mortality rates when current habitat quality of highly revisited sites is not optimal or even declining. Insectivorous birds are rapidly declining (Bowler *et al.* 2019), emphasizing the need to prevent unsustainable farming practices and to control climate change to maintain insect biodiversity (Raven & Wagner 2021), which is also the main food source for Northern Bald Ibis, and which would also be essential for the survival of numerous other species and may be directly beneficial to agriculture itself. Thus, identification of seasonally revisited habitats, such as foraging areas, is essential in order to foster long-term monitoring and protection of relevant areas.

In sum, our results from the semi-wild Northern Bald Ibis colony observed in this study have quite some potential for informing conservation and reintroduction programs because they show the influence of individual traits on spatio-temporal patterns and the importance to conserve existing foraging and roosting areas that are frequently used by this threatened species.

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Conflict of interest

None.

Ethical standards

All authors adhered to the 'Guidelines for the use of animals in research' as published in Animal Behaviour (1991, 41, 183–186). This study complies with all current Austrian laws and regulations concerning work with wildlife. Experimental setup was performed under Animal Experiment Licence Numbers BMWFW-66.006/0011-WF/II/3b/2014 and BMWFW-66.006/0026-WF/V/3b/2014 by the Austrian Federal Ministry for Science and Research. Birds were habituated to the presence of humans.

Supplementary Material

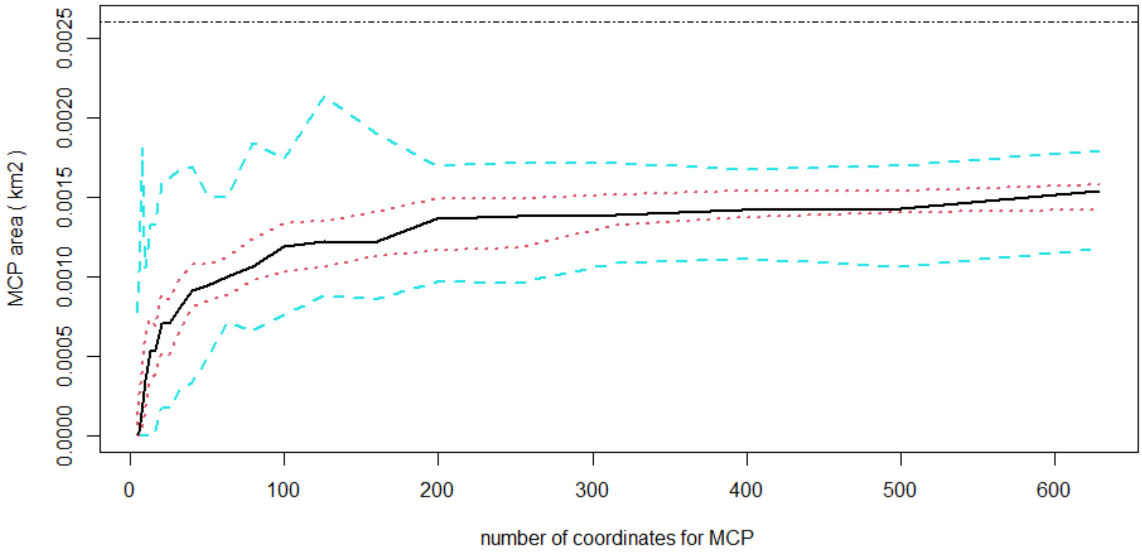

Figure S1. Minimum convex polygon (MCP) area of the breeding season by a logarithmic step wise increase of the number of GPS points per calculation. 0% percentile of MCP area – blue bottom line, 25% percentile of MCP area – red bottom line, 50% percentile of MCP area – black middle line, 75% percentile of MCP area – red top line, 100% percentile of MCP area – blue top line, real MCP area size of all locations – horizontal dot-dashed black line.

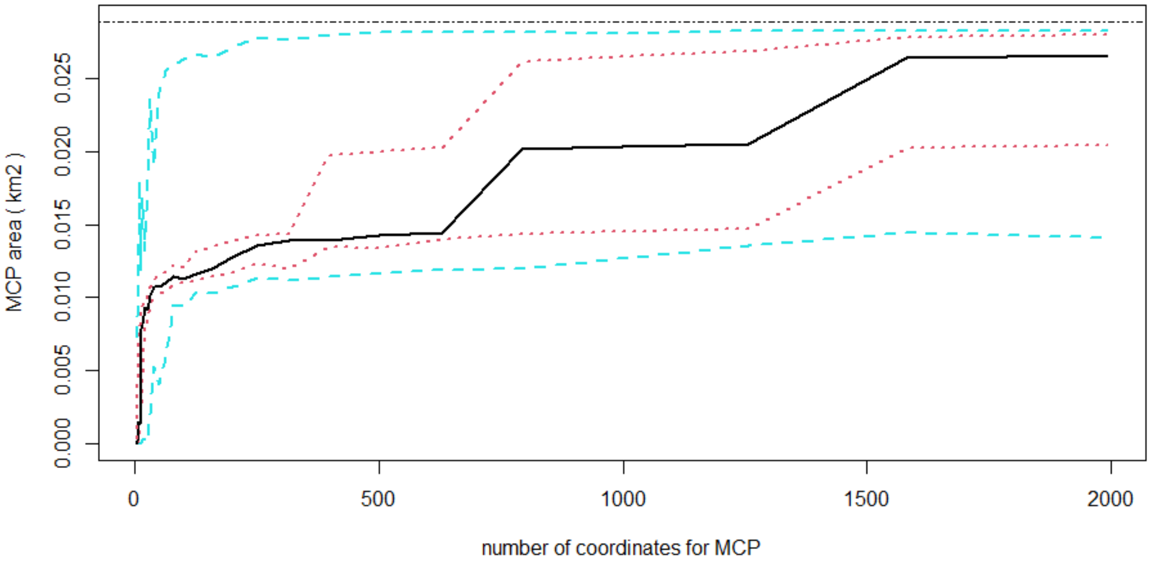

Figure S2. Minimum convex polygon (MCP) area of the non-breeding season by a logarithmic step wise increase of the number of GPS points per calculation. 0% percentile of MCP area – blue bottom line, 25% percentile of MCP area – red bottom line, 50% percentile of MCP area – black middle line, 75% percentile of MCP area – red top line, 100% percentile of MCP area – blue top line, real MCP area size of all locations – horizontal dot-dashed black line.

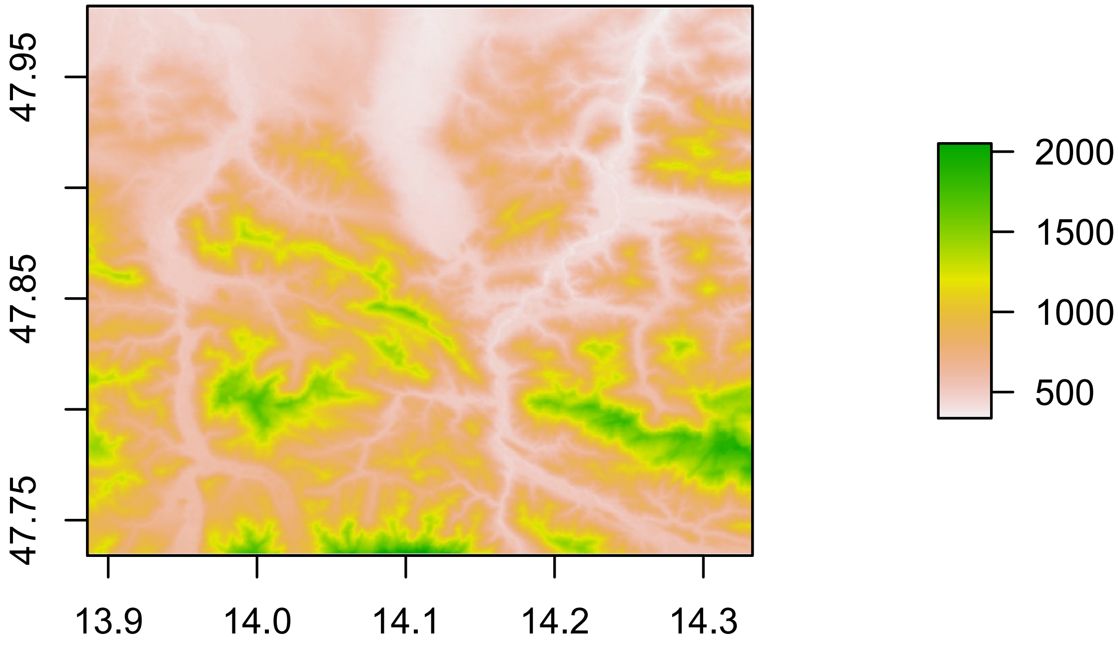

Figure S3. Elevation variable used to model step-selection function. Elevation is given in meters. Global digital elevation model (spatial resolution 1 arc second, 30 m) derived using the environmental-data automated track annotation (Env-DATA) System of Movebank.

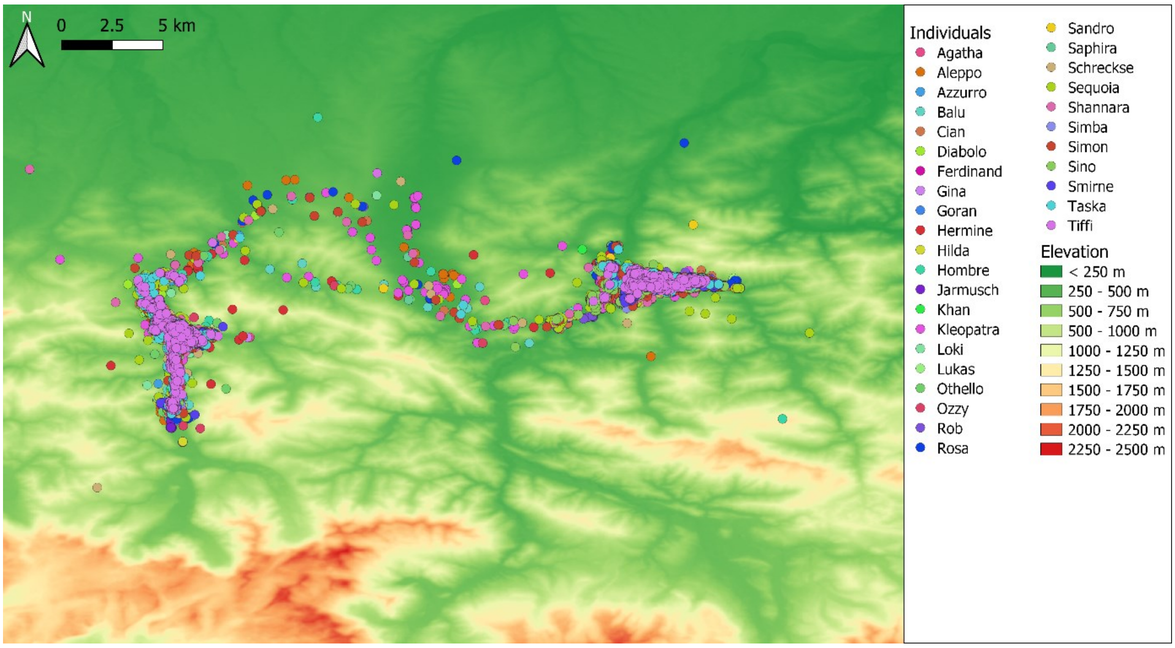

Figure S4. Flyways between study areas. The coloured dots represent the individuals. Background digital elevation model (DEM) was derived from oe3d in spatial resolution 1 arc second (approximately 20-30 m, http://www.oe3d.at/).

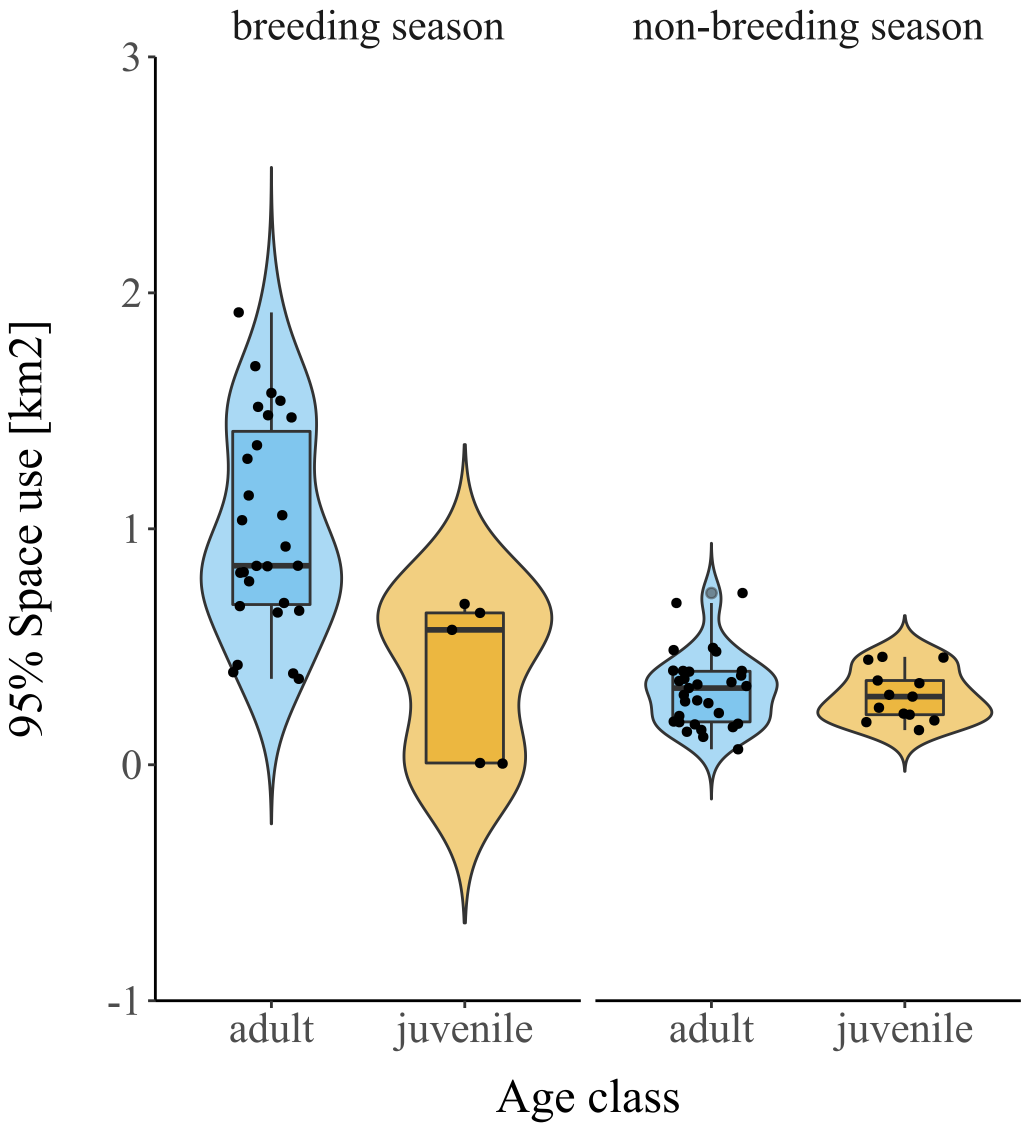

Figure S5. Space use [95%, km²] separately for each combination of age class and season.

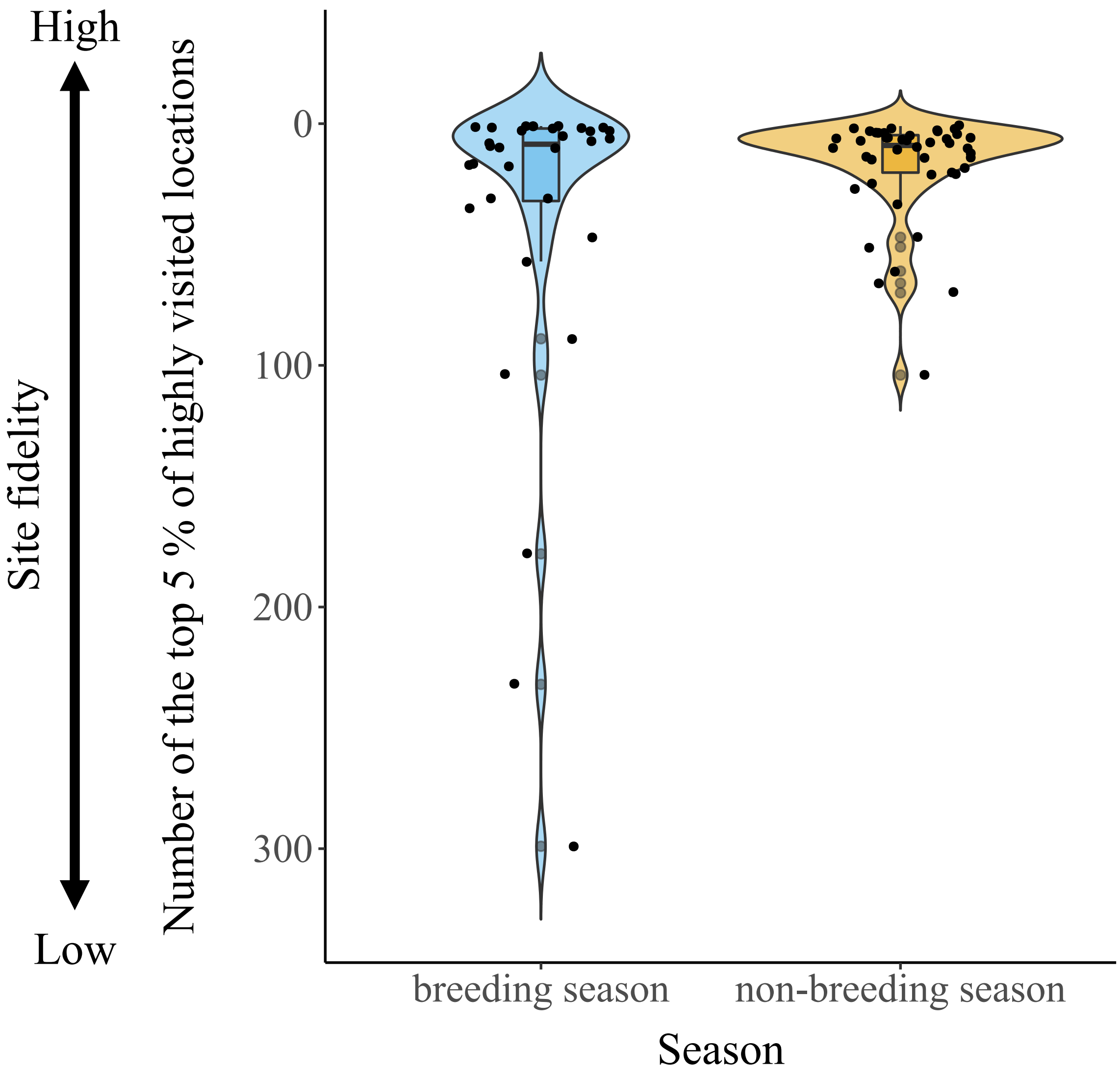

Figure S6. Site fidelity (number of top 5% of highly visited locations) as a function of season (i.e. breeding and non-breeding season). High site fidelity depicts low number of revisited locations, while low site fidelity depicts high number of revisited locations.

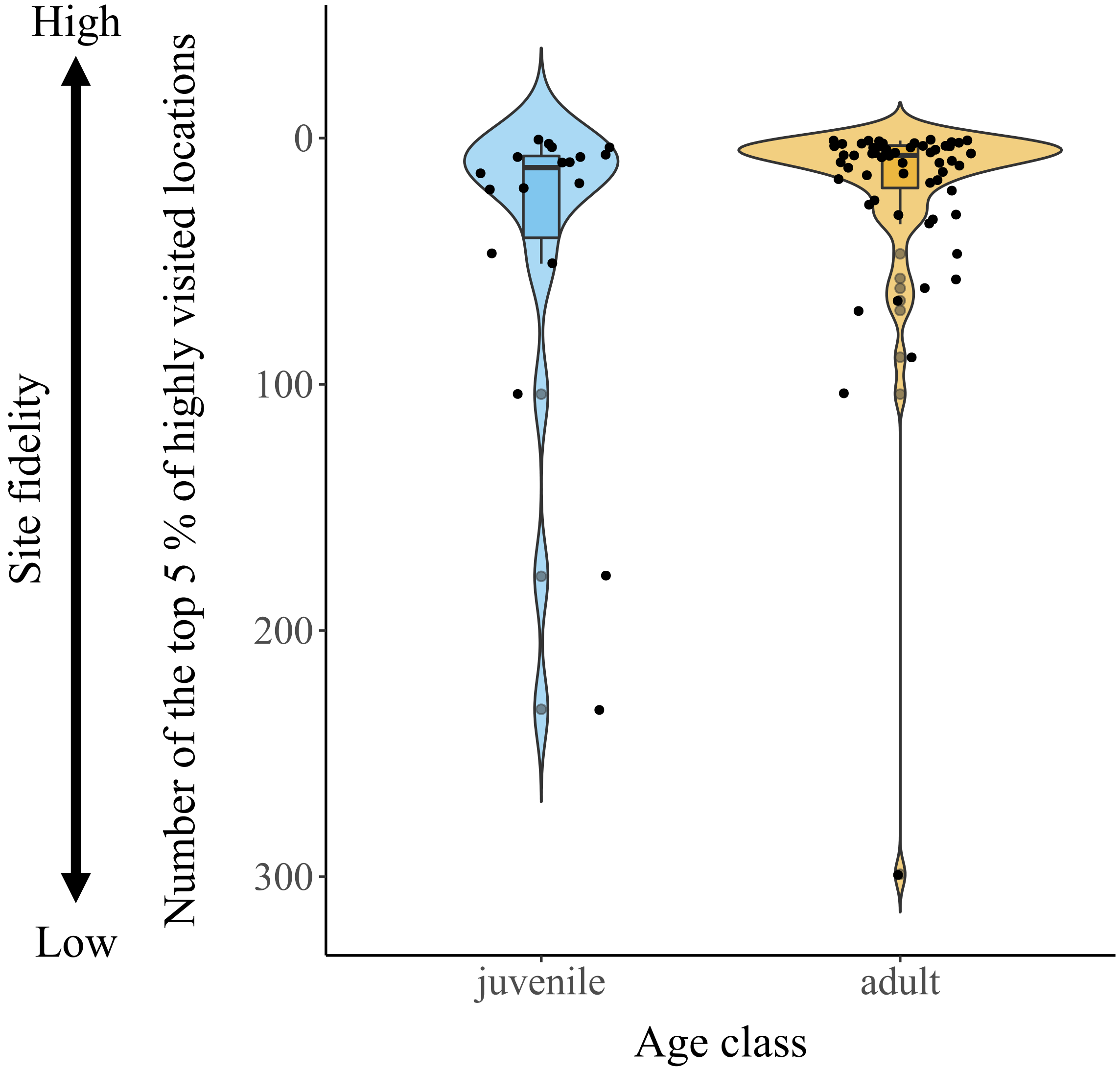

Figure S7. Site fidelity (number of top 5% of highly visited locations) as a function of age (i.e. juvenile and adult). High site fidelity depicts low number of revisited locations, while low site fidelity depicts high number of revisited locations.

CONCLUDING DISCUSSION

1. Method validation

1.1. Summary of results

Chapter I adds to the knowledge of which enzyme immunoassay to use to accurately measure excreted glucocorticoid metabolites in the Northern Bald Ibis. Despite the fact that the enzyme immunoassay ‘corticosterone' has previously been used for Northern Bald Ibis droppings (e.g. Sorato & Kotrschal 2006), the enzyme immunoassay ‘11-oxoaetiocholanolone' proved to be the most suitable. Compared to other assays, this one was far more sensitive and detected peaks in the concentrations of excreted corticosterone metabolites over a longer period after stress was induced by handling the birds, whereas the previously used enzyme immunoassay detected only the first peak concentration.

Chapter III contributes to the knowledge on the effects of tracking devices on individual birds. The findings of this study revealed that (1) bio-loggers had no effect on individual behavioural phenotypes in terms of maintenance behaviour, dorsal feather preening, locomotion, and foraging, (2) GPS-tagged birds had fewer affiliative interactions than control birds directly after tagging, but frequencies increased shortly thereafter, and (3) excreted corticosterone metabolite concentrations remained elevated 1 month after tagging.

1.2. Enzyme immunoassay validation

Non-invasive monitoring of hormones is an essential tool in ecology and conservation, in particular when studying animals in the wild. A recent study in Northern Bald Ibis used feather corticosterone concentrations to infer about subsequent reproductive success (Monclús *et al.* 2020). However, these feathers were pulled during routine medical examinations, which just like blood sampling would not be feasible for wild populations. In my opinion, non-invasive measurement of glucocorticoid metabolites remains the most suitable method for free-ranging animals and is an essential tool for conservation studies, as it aids the understanding of reproductive biology, pregnancy diagnostics and welfare of wildlife

(Kumar & Umapathy 2019). But accurate measurements of excreted hormone metabolite concentrations using validation procedures (Palme 2005, 2019; Sheriff *et al.* 2011; Touma & Palme 2005) are relevant when using conservation physiology in the wild to inform conservation management.

However, even with a validated enzyme immunoassay, the results have to be interpreted with caution as non-invasive monitoring can also be influenced by several other confounding factors, such as time of day, season, sex, diet, metabolic rate or bacterial degradation (Goymann 2012), which have to be considered in data collection. Time of day was controlled for in the present study, as droppings were only collected within a certain time period. Diet as well as metabolic rate can differ between seasons and can be decisive for differences in hormone metabolite concentrations (Goymann 2012). This was not the case in the present study, as droppings were collected from May till October, during which both temperature and food availability, as well as food type and quality, are comparable. However, I did not account for intraspecific variation in metabolic rate (Norin & Metcalfe 2019), which could have influenced the results of this study. As the enzyme immunoassay for Northern Bald Ibis has been validated for both sexes and both females and males show relatively similar behavioural and physiological patterns (Sorato & Kotrschal 2006), sex-specific adequate interpretations of hormone metabolite measurements can be made. Furthermore, excreted metabolite levels vary from dropping to dropping (Goymann 2012; Scheiber *et al.* 2005a); thus, multiple samples per individual are required to measure accurate excreted metabolite concentrations. Sample collection of the present study would need to be improved as the collection of several droppings in the field was sometimes not possible.

1.3. Effects of bio-loggers: Tracking birds

Most studies investigated whether tracking devices have a negative impact on survival rate (Barron *et al.* 2010; Bodey *et al.* 2018), but paid little attention to the effect on behaviour and physiology. Behavioural interactions and excretion patterns of corticosterone metabolites in the Northern Bald Ibis were only altered on a short-term period, suggesting to include an adaptation phase in study design prior to data collection to reflect the natural behaviour and physiology accurately.

Apart from potential effects on study results, this is especially important for free-ranging animals, as direct observations of these individuals are often not possible (Barron *et al.* 2010; Bodey *et al.* 2018). In particular, because changes related to tracking devices may affect reproduction, not least because one of the most substantial effects of GPS tagging in other studies is the decreased likelihood of nesting (Barron *et al.* 2010). Arctic Terns (*Sterna paradisaea*), however, did not seem to be affected by the GPS transmitter itself but rather by the capture and handling procedure: individuals experiencing capture and handling had lower brood-provisioning rates (Seward *et al.* 2021). Similarly, in a free-ranging breeding seabird, the Manx Shearwater (*Puffinus puffinus*), GPS tagging was linked to altered foraging behaviour during incubation; but these behavioural changes did not have long-term fitness consequences (Gillies *et al.* 2020). However, higher energy expenditure owing to tracking devices during winter (Pennycuick *et al.* 2012) may result in reduced energy available for reproduction, such as building a nest, producing eggs, and raising chicks. Rapid advances of cutting-edge tracking devices create a need to assess the potential impacts of such devices on individual birds (e.g. changes to behaviour) and consequently on the results of studies as tagging may bias the data collected (Harris *et al.* 2012).

I did not observe any detrimental effects (i.e. weight loss, skin abrasion or other injuries) in the study colony, although GPS transmitters have been linked to unilateral corneal opacity in two other Northern Bald Ibis populations (in both studies, GPS transmitters were backpack mounted with a harness; Fritz *et al.* 2020). However, as I did not investigate long-term effects of tracking devices on the endangered Northern Bald Ibis, I can only infer about intermediate effects. Still, this study showed that disrupted behavioural patterns and physiology returned to baseline levels after a short time period. Thus, it seems that free-ranging animals need to be carefully monitored in the first months after tagging. This shows the importance of not only considering social behaviour but also physiological parameters when investigating effects of bio-loggers. However, as other studies reported definitive effects on survival, body condition, flying ability, reproduction or parental care (Barron *et al.* 2010; Bodey *et al.* 2018; Lameris *et al.* 2018; Tomotani *et al.* 2019), investigating long-term effects would be of great importance.

2. Part I: Physiological implications of social behaviour

2.1. Summary of results

The results presented in **Chapter I** reflect seasonal differences (i.e. reproductive and post-reproductive season) in physiology (i.e. excreted corticosterone metabolites, endoparasite burden) and the ability to buffer high energetical costs of the reproductive season with affiliative interactions. I found (1) more frequent affiliative social interactions during the reproductive season compared to the post-reproductive season, (2) higher levels of excreted corticosterone metabolites during the reproductive season than during the post-reproductive one, which was mirrored by decreasing endoparasite burden, and (3) paired individuals excreted fewer samples containing coccidian oocysts compared to unpaired individuals.

Chapter II provides evidence for strong seasonal differences in patterns of proximity and social behaviour in the endangered Northern Bald Ibis. Specifically, I recorded (1) greater proximity in autumn compared to winter, (2) no season-dependent variation in agonistic behaviour, but males were involved in more agonistic interactions than females, (3) more affiliative interactions in winter, and females received more frequently affiliative behaviours than males, (4) that affiliative interactions are more likely to occur between former and potentially prospective reproductive partners than between other conspecifics, and (5) an age-dependent centrality of social positions, with younger individuals occupying less central social positions and receiving agonistic behaviours more frequently.

2.2. The role of affiliative behaviour: Partners with benefits

Due to co-evolution of host-parasite interactions, vertebrates typically do not suffer from long-term increases in glucocorticoids in response to parasitic infections (Sapolsky *et al.* 2000). This was also obvious in the current study system, as the Northern Bald Ibis did not show prolonged elevated excreted corticosterone metabolite concentrations and endoparasite burden. However, the secretion of low glucocorticoid levels may also be linked to possible pathology (O’Dwyer *et al.* 2020), as the HPA feedback loop may suppress the release of glucocorticoids in response to a chronic stressor (Herman et al. 2011). During energetically costly time windows, such as the reproductive season (Romero 2002), individuals face various stressors, which lower the immune response against primary or even secondary parasitic infections (Hing *et al.* 2016) and thus have important fitness consequences (O'Dwyer *et al.* 2020). Individuals may face a trade-off between allocating energy to reproduction or to maintaining a well-functioning immune system during the reproductive season, as evidenced by high endoparasite load and high excretion of corticosterone metabolites (Sheldon & Verhulst 1996).

I discovered that during periods of high corticosterone metabolite excretions affiliative interactions between breeding partners may have buffered endoparasite burden, indicating an upregulation of the immune response. Thus, affiliative interactions seemed to buffer high energetical costs of the reproductive season. Previously published studies have reported that familiarity between individuals increases the social buffering effect (Kiyokawa *et al.* 2014; Rukstalis & French 2005; Wittig *et al.* 2016). Thus, the quality of the relationship between the interacting individuals plays a major role and determines whether a stress response can be mitigated (Kiyokawa & Hennessy 2018). However, excreted corticosterone metabolite levels did not seem to be influenced by affiliative interactions. The results of this Chapter suggest that strong affiliative ties may alleviate endoparasite load and thus have a positive effect on the immune system.

2.3. Factors affecting social relationships: Younger birds on the social edge

The position an individual holds within a social network is important for the social structure (Lusseau & Newman 2004). In Northern Bald Ibis, young individuals seemed to occupy less socially central positions than adult individuals. Similar patterns have also been found in African elephants (*Loxodonta africana*), in which older females occupied more central positions and older males maintained greater stability in their position (Murphy *et al.* 2019). Individuals occupying more central positions within a social network are important for maintaining network structure and group cohesion (Flack *et al.* 2005, 2006) and more central positions are associated with fitness benefits (Cheney *et al.* 2016; Ellis *et al.* 2017; Ryder *et al.* 2009; Stanton & Mann 2012).

Seasonal variations in social dynamics may occur because of reproductive seasonality (Brent *et al.* 2013), which drives seasonal fission-fusion dynamics (Silk *et al.* 2014). Changes in inter-individual distance and affiliative behaviour were observed between autumn and winter in the present study. However, these variations in social dynamics reflect differences in pair bond stability and start of pair formation rather than fission-fusion dynamics, as fission-fusion is not very distinctive in Northern Bald Ibis. Social dynamics can influence many factors, such as maintaining cooperation (Cronin & Sánchez 2012; Werdenich & Huber 2002) and disease transmission dynamics (Wilson *et al.* 2020). Disease transmission risk may mirror seasonal dependent social dynamic patterns, because affiliative interactions may either impact the risk of infection in the social network (Balasubramaniam *et al.* 2016; Wilson *et al.* 2020) or alleviate disease susceptibility through social buffering (Balasubramaniam *et al.* 2016).

3. Part II: Movement ecology in social animals

3.1. Summary of results

The results presented in **Chapter IV** provide insight into one of the key domains of behavioural ecology – movement ecology – broadening our understanding of the individual and seasonal factors that determine an endangered species' use of space and site fidelity. The data reflect consistently high site fidelity and overlapping space use between individuals over successive years. Furthermore, (1) individuals flew along valleys rather than through mountainous areas when they moved between different areas, (2) adults used more space during the breeding season than during the non-breeding season, but this effect was not as strong for juveniles, (3) individuals generally had higher sight fidelity during the non-breeding season and site fidelity was stronger in adult birds compared to juveniles, (4) space use and site fidelity did not vary by sex.

3.2. Factors affecting space use and site fidelity: Site fidelity is age-dependent

Space-use patterns of the study colony were comparable with the western resident population in Morocco (Bowden *et al.* 2008), but more restricted compared to the migratory eastern relict population (i.e. Syria, Serra *et al.* 2011, 2013). Thus, differences in space use patterns to wild populations are not primarily a consequence of food supplementation, but rather due to climate conditions (Bowden *et al.* 2003) and habitat degradation of the Syrian steppe (Serra *et al.* 2009) and thus a lack of efficient detection of suitable foraging areas. This may also be one of the main factors leading to the rapid decline of the Syrian population, while the Moroccan population size is increasing and somewhat stabilizing after applying specific conservation actions (Smith *et al.* 2008).

Intraspecific variation in space use patterns has been related to different factors, such as sex (Aronsson *et al.* 2016; Ofstad *et al.* 2019), age (Šklíba *et al.* 2016), reproductive status (Aronsson *et al.* 2016; Wikenros *et al.* 2016), habitat quality (Betts *et al.* 2008; Bjørneraas *et al.* 2012) or population density (Kjellander *et al.* 2004). As the Northern Bald Ibis is a species that tends to operate in flocks with groups of birds feeding and moving together, consistent space use patterns and site fidelity to specific locations may be expected. However, I found seasonal and age-specific differences in space use patterns in Northern Bald Ibis, which may have been linked to offspring provisioning foraging strategies in adults and dispersal related space use patterns in juveniles. Seasonal variation in space use is often associated with food availability (Kolts & McRae 2017; Rolstad & Rolstad 1995); but, food availability alone cannot explain the patterns found in this study, as I did not collect data during winter. Thus, food availability was expected to be the same across data collection. Variation in seasonal space use patterns highlights the importance of investigating the Northern Bald Ibis year-round. Furthermore, sexual segregation in habitat use was reported in several other species (Kolts & McRae 2017). Northern Bald Ibis are hardly sexually dimorphic and spend most of their time in a group (Böhm & Pegoraro 2011), which explains the similar space use patterns in both males and females.

Consistent use of specific movement corridors and generally high site fidelity to specific locations in Northern Bald Ibis reflect stability in space use patterns (Harris & Leitner 2004). Stability in space use patterns drives reproductive success, with birds that have higher site fidelity having higher reproductive success (Patrick & Weimerskirch 2017). For instance, small local populations of snubfins (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*) in the coastal waters of Australia show preferential use of specific areas, probably because of higher foraging and reproductive success associated with these areas (Parra *et al.*

2006). However, site fidelity can also entail certain risks, especially in urban environments, where animals may be exposed to poison or other anthropogenic effects (Santangeli *et al.* 2019; Serieys *et al.* 2019).

4. Chapters integration and limitations

4.1. General conclusion: Relevance for conservation

In my thesis, I integrated different aspects of behavioural ecology with regard to social behaviour and movement ecology, broadening our understanding of the link between affiliative behaviour and physiology and factors that shape space use and site fidelity patterns. The findings contribute to a better understanding of how social relationships and social positions of individuals could help to select specific individuals for reintroduction and how seasonal trends in habitat use are associated with behaviour, age-related mortality risk associated with different positions within the social network, and not least the role of male affiliative behaviour for pair bond formation. The resulting biologically relevant data may be useful to inform conservation actions and generate strategic conservation recommendations as Northern Bald Ibis were found to be conservative in space use and younger individuals had fewer affiliative ties, which could impact recruitment and reintroduction projects. A key aspect for developing new or improving existing conservation actions is to investigate different domains of behavioural ecology, which are interlinked with each other. The Northern Bald Ibis could be used as a flagship or umbrella species, as results of the present studies could provide information for conservation actions of species with similar biological and ecological requirements.

Almost half of the world's bird populations are already declining (BirdLife International 2018b; Rosenberg *et al.* 2019). Gaining knowledge on social dynamics and structure (Webber & Vander Wal 2019), as well as space use (Vaudo *et al.* 2014) and site fidelity patterns (Warkentin & Hernández 1996) are relevant to better manage threatened populations and species, respectively. For instance, protecting key bird and biodiversity areas would conserve resources at the site level. However, protection of such areas alone is not sufficient for effective conservation. Habitats need to be restored to reconnect landscapes (BirdLife International 2018b).

Conservation benefits of such studies in direct relation to the protection of habitat and movement corridors, harvest management, and mechanisms of climate change impacts on populations (Hebblewhite & Haydon 2010).

Behavioural ecology studies can aid wildlife conservation by generating new knowledge on the structure and function of social groups and how animals respond to environmental changes on the individual and population level (Berger-Tal *et al.* 2011). On an extended level GPS-based technology can be linked to behavioural and social network studies to track interactions among individuals and important changes in the social system, to make inference about the vulnerability of a population (Dougherty *et al.* 2018; Snijders *et al.* 2017), to monitor endangered species, their threats and to protect their habitats (Berger-Tal & Lahoz-Monfort 2018; Schofield *et al.* 2007), to detect poaching events (O'Donoghue & Rutz 2016), to investigate the distribution of animals in combination with resource use within their environment (Kays *et al.* 2015), and the impacts of humans or environmental changes on animal movement (Hebblewhite & Merrill 2008). GPS-based technology also aids modelling predicted habitat loss and distribution of individuals due to climate change (Durner *et al.* 2009). Behavioural indicators, such as home range use, habitat selection or foraging and patch use behaviours, and physiological parameters, such as glucocorticoids, reproductive steroids or energy expenditure, can be used to assess the vulnerability status of a population (e.g. impending population crash or social fragmentation) or whether conservation actions are effective or in need of adaptation (Berger-Tal *et al.* 2011; Wikelski & Cooke 2005). For instance, prolonged secretion of glucocorticoids induces an increase in oxidative stress, which is assumed to affect fitness and susceptibility to disease (Costantini *et al.* 2011). Stress-induced negative effects on behavioural flexibility, spatial reference or memory could also impair an individual's survival in a rapidly changing environment (Dias-Ferreira *et al.* 2009). Thus, understanding behavioural variation related to group-level attributes is crucial for conservation management (Bengston & Jandt 2014; Estrada *et al.* 2017), in particular because stress load can differ depending on sex and age (McEwen 2002).

In the following subsections, I discuss the importance of my results in relation to potential conservation implications of (1) the role of affiliative interactions on physiology, (2) the social position within a group, (3) GPS transmitters, and (4) a better understanding of space use and site fidelity patterns.

4.1.1. Conservation implications of the role of affiliative interactions on physiology

First, I have validated an enzyme immunoassay for non-invasive measuring of excreted glucocorticoid metabolites in Northern Bald Ibis. With the best-suited assay I investigated the role of affiliative behaviour in relation to energetically costly and stressful periods. Chronic elevated glucocorticoid release during reproduction could inhibit reproduction or even cause abortions or brood abandonment (Ouyang *et al.* 2012; Young *et al.* 2006) as well as affect survival (Sapolsky *et al.* 2000), which could have detrimental effects on the viability of populations; in particular for threatened and declining species. Conservation physiology proposes that glucocorticoid concentrations can contribute to the status assessment of populations. Increased glucocorticoid secretion may be an indicator for a more challenging environment. Thus, measuring physiological stress responses could also be used to assess the influence of human activities on wildlife (Wikelski & Cooke 2005). Stress physiology is one out of many physiological sub-disciplines contributing to conservation science. This sub-discipline allows to infer about reactions to environmental changes or to monitor the success of reintroduction programmes. In combination with immunology/epidemiology one can further infer about disease spread and how to manage those. The conservation physiology toolbox is an essential tool for managing threatened species, for instance to monitor the link between immune response and disease susceptibility or population decline (Madliger *et al.* 2018, 2021; Wikelski & Cooke 2005). As infectious diseases can impact wildlife management, social buffering has important implications for conservation and thereby may provide a way to reduce disease spreading and transmission. For instance, strong affiliative ties can reduce physiological stress responses (Sachser *et al.* 1998) and thereby increase survival and reproductive success (Wascher *et al.* 2019; Wu 2021). This suggests that the social buffering hypothesis may aid conservation efforts, such as translocation or reintroduction projects where individuals are confronted with novel environments that may elicit physiological stress responses (Hennessy *et al.* 2006; Pinter-Wollman *et al.* 2009).

Individuals with strong affiliative bonds may mitigate physiological stress responses to environmental changes and relocation processes. Thus, prior to such an action, conservationists need to be aware of the social structure to make decisions in favour of individual well-being, as behavioural indicators can be used to indicate early stages of population decline (Searle *et al.* 2007; van Gils *et al.* 2009) and to monitor the success of conservation actions (Ikuta & Blumstein 2003; Lindell 2008).

4.1.2. Conservation implications of the social position within a group

To further investigate patterns of relationships (i.e. social dynamics and structure) within a colonial breeding bird species, I next investigated factors shaping social dynamics. Social network analysis presents an excellent tool for conservation management to monitor changes in social dynamics and to design according conservation actions. During these observations, I discovered sex-related differences in the investment into pair bond maintenance, age-specific centrality positions within the social network, and that social relationships modulate inter-individual distance. These findings of sex- and age-related differences contribute to understanding factors associated with breeding success and mortality risk in an endangered bird species. Age-related centrality positions in the Northern Bald Ibis could be relevant information for conservation actions and reintroduction projects, as it seems that younger individuals may be less optimal for reintroduction due to greater mortality and dispersal risk linked to their less central position within the network. However, when using social network analysis to assess conservation actions (e.g. relocation of individuals) or the vulnerability of a population (Snijders *et al.* 2017), several factors, which can have an impact on the social dynamics of a group, need to be considered: for instance the impact of removing individuals from a social group (Flack *et al.* 2006; Lehmann & Dunbar 2009), manipulating the sex ratio (Darden *et al.* 2009; Jacoby *et al.* 2010) or time spent together within a group (Corner *et al.* 2003), as well as environmental changes (e.g. food abundance, Foster *et al.* 2012) or variations in group size (Lehmann & Boesch 2009). Furthermore, disease transmission dynamics could also be altered by the seasonal modularity of affiliative ties (Springer *et al.* 2017). A potential implication of this is the importance of examining group structure prior to selecting specific individuals for reintroduction projects. As some individuals (i.e. younger individuals) may face higher mortality and dispersal rates due to occupying less socially central positions, assembling individuals with stable social relationships is crucial to successfully establish self-sustaining and sedentary colonies with high reproductive success.

4.1.3. Conservation implications of GPS transmitters

Combined with movement analyses one can further address questions regarding the vulnerability of a population. Data obtained by tracking devices can be essential for conservation management, as these data make the detection of illegal causes of mortality (Sergio *et al.* 2019) or the protection of habitats by identifying potential disturbances at breeding sites due to built infrastructure (e.g. wind farms, power lines) possible (Veltheim *et al.* 2019). On the one hand, to ensure well-being, safety, ethical regulations and to keep possible effects at a minimum, identifying potential effects of tracking devices on behaviour and physiology is of particular importance to carefully consider whether to equip individuals with bio-loggers, which attachment method to use, and the placement of the bio-logger on the body (Geen *et al.* 2019). On the other hand, there are still some constraints in the application of tracking devices in conservation biology, such as the accuracy of GPS transmitters, data availability, transmission issues in remote areas as well as validation of telemetry data, effective implementation of movement ecology in conservation actions, and improved communication between scientists and conservation managers (Katzner & Arlettaz 2020). To evaluate possible adverse effects of bio-loggers in Northern Bald Ibis, I designed an experiment that showed that tracking devices had no impact on maintenance behaviour, dorsal feather preening, locomotion, and foraging; but, tagged individuals had short-term elevated excreted corticosterone metabolite levels after tagging.

4.1.4. Conservation implications of a better understanding of space use and site fidelity patterns

In the final chapter of my dissertation, I analysed factors that shape space use and site fidelity patterns. I found season- and age-specific space use and site fidelity and individuals to be extremely consistent in their patterns of space use. The seasonal- and age-specific differences in movement and space use patterns in

Northern Bald Ibis suggest to implement age-specific approaches to managing movement and space use in both age classes. This information can be used to improve the protection of existing conservation habitats, but also to identify new habitats of conservation concern. Movement and space use patterns generally inform about the vulnerability of threatened and declining species, productivity of available habitats, habitat restoration actions, collision possibilities with infrastructure, movement of invasive species, distribution of resources and limiting factors and how species use resources. Thus, GPS-based technology is an important aspect of conservation science (Berger-Tal & Lahoz-Monfort 2018). This also aids the assessment of different reintroduction strategies, the viability and vulnerability of a population in a particular habitat and informs about the potential distribution range of a species (e.g. Macdonald *et al.* 2000; Macdonald & Rushton 2003).

Site fidelity could impact the viability of a population due to habitat degradation and loss, in particular when species inhabit restricted habitats (Warkentin & Hernández 1996). To counteract population decline associated with high site fidelity, threatened and declining species displaying site fidelity need to be monitored and conservation actions need to be adapted. In addition, tailored conservation strategies must take effect depending on the level of site fidelity of a species or population (Schlossberg & King 2007; Theobald *et al.* 2000). For instance, site fidelity needs to be considered when translocating individuals. Gopher tortoises (*Gopherus polyphemus*) seemed to increase site fidelity while being kept in enclosures for a certain time prior to relocation, suggesting that the use of enclosures could be an essential step in relocation projects to establish self-sustaining populations (Tuberville *et al.* 2005).

Space use and site fidelity patterns are closely linked to the social structure and dynamics of wildlife populations, as high movement rates increase gene flow, whereas site fidelity increases genetic structure (Slatkin 1987). Thus, small populations are more vulnerable to extinction compared to large stable populations because of loss of gene flow and variability in environment and population size (Caughley & Gunn 1996). Populations with high site fidelity could face higher mortality rates when current habitat quality of highly revisited sites is not optimal or even declining. Movement ecology is an essential aspect of the behavioural ecology of many species (Berger-Tal *et al.* 2011) and is relevant to develop conservation actions to increase sustainability and viability of populations (Dizon *et al.* 1992; Moritz 1994).

4.2. Limitations of the research

Some limitations should be noted. First, the correlative nature of the data in **Chapter I** limits the inference about the role of affiliative interactions in the context of physiological stress responses. This underscores the need for experimental studies to generate a clear picture about sex-specific differences and the complex relationships between elevated glucocorticoids, endoparasite burden and immune system and how affiliative interactions may buffer physiological stress responses. Second, in **Chapter II** only two seasons were considered in the social network analysis. To get a clear picture which factors affect patterns of relationships in a globally endangered bird species and consequently to inform conservation actions, annual patterns in social dynamics and structure are needed. Third, in **Chapter IV**, only some individuals were tracked over successive years, which would be valuable to infer about individual adaptations in space use and site fidelity patterns due to environmental changes. Thus, to generate knowledge on habitat predictability and stability, and to inform about species' vulnerability, one would need to collect individual long-term data, as each individual of a threatened species is disproportionally important.

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