

Causes, patterns and consequences of movement in Arctic avian predators

**Doctoral thesis for obtaining the
academic degree**

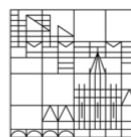
*Doctor of Natural Sciences
Dr.rer.nat.*

submitted by

Curk, Teja

at the

Universität
Konstanz



Faculty of Sciences
Department of Biology

Date of the oral examination: 4.11.2021

First reviewer: prof. dr. Martin Wikelski

Second reviewer: prof. dr. Nicolas Lecomte

Konstanz, 2021

*Look closely at nature. Every species is a masterpiece,
exquisitely adapted to the particular environment
in which it has survived. Who are we to destroy
or even diminish biodiversity?*

E. O. Wilson

i

Discussion	55
Acknowledgements	58
Chapter 4 Arctic avian predators synchronise their spring migration with the northern progression of snowmelt	60
Abstract	61
Introduction	62
Methods	64
Results	68
Discussion	70
Acknowledgements	76
Chapter 5 Wing tags severely impair movement in African Cape Vultures	77
Abstract	78
Background	79
Results	81
Discussion	89
Conclusions	92
Methods	93
Acknowledgements	96
General discussion	97
Appendix 1 Supplementary material to Chapter 1	103
Appendix 2 Supplementary material to Chapter 2	106
Appendix 3 Supplementary material to Chapter 3	115
Appendix 4 Supplementary material to Chapter 4	119
Appendix 5 Supplementary material to Chapter 5	128
References	134
Author contributions	150
Acknowledgements	152
List of publications	154

Summary

Animal movement has a great impact on populations, species communities, even entire ecosystems. The reasons for moving are different and include foraging, searching for mates, reproduction, and avoiding predation. All these movement decisions at the individual level define the fate of an animal. The rapid development of tracking technologies advanced our understanding of movement ecology and helps us to investigate the causes, patterns and consequences of movement in animals.

During my PhD, I investigated different aspects of animal movement, using birds as a model organism. In the first chapter, I studied the causes of irregular massive movement in snowy owls (irruptions) and consequences for their body condition. The results showed that winter irruptions in snowy owls might be a strategy to maintain body condition when resources on the breeding grounds become limited due to the large number of offspring produced in a current breeding season.

In the second chapter, I characterized nomadism vs regular migration, which are different movement patterns expressed by snowy owls and investigated the causes for the contrasting movement patterns and their consequences in terms of energy intake. The study demonstrated that the different movement patterns found between individuals could be a response to the different resource variability they encounter in the environment and serve to secure comparable levels of resources i.e. potential for energy intake.

In the third chapter, I looked at the causes of movement concerning resource variability and breeding success in rough-legged buzzards and the patterns of movement with regard to searching to prospect for a nesting site during the previous breeding season. The results suggested that rough-legged buzzards compensate for the lack of time by selecting the nesting location already during the previous breeding season and that breeding success and resource stability influence the amount of prospecting movement i.e potential search for the nesting location for the following year.

In the fourth chapter, I assessed the consequences of movement patterns, specifically proximate responses to environmental conditions in three Arctic raptor species. The study demonstrated that all three species followed the northern progression of snow melt during

the spring migration suggesting that they use snow conditions as a cue to time their arrival at the breeding grounds. The snowy owl and the rough-legged buzzard having high movement flexibility had a stronger response to the snow conditions than the peregrine falcon with less flexible movement.

Finally, in the fifth chapter, I investigated the human-induced causes of movement as a consequence of the tag attachment on animals. The results provide evidence that the tagging method affected flight performance in South-African cape vultures and suggested that patagial tags cause adverse effects on the endangered vulture species. This is of great importance for the well-being of the species as well as for the quality of the collected data which can be biased and cause misinterpretation of the observed behaviour.

These findings not only help us to understand the movement ecology of animals but also have important implications for the conservation of the species. The next step is to further investigate how individuals track and use the environment since this knowledge can help us to predict the impact of future environmental change. We will be able to understand how climate change affects movement decisions on a smaller scale as well as movement patterns which would help us to identify the species in need of management actions.

Zusammenfassung

Tierbewegungen haben einen großen Einfluss auf Populationen, Artengemeinschaften und sogar ganze Ökosysteme. Die Gründe für die Bewegung sind unterschiedlich und umfassen die Nahrungssuche, die Suche nach Partnern, die Fortpflanzung und die Vermeidung von Raubtieren. All diese Entscheidungen, die Individuen bezüglich ihrer Bewegung treffen, bestimmen ihr Schicksal. Die rasante Entwicklung von Tracking-Technologien hat unser Verständnis der Bewegungs-Ökologie vorangetrieben und hilft uns, die Ursachen, Muster und Folgen von Bewegungen bei Tieren zu untersuchen.

Während meiner Doktorarbeit untersuchte ich verschiedene Aspekte der Tierbewegung, wobei ich Vögel als Modellorganismus verwendete. Im ersten Kapitel untersuchte ich die Ursachen unregelmäßiger massiver Bewegungen bei Schnee-Eulen (Irrruptionen) und die Folgen für ihren physischen Zustand. Die Ergebnisse zeigten, dass Irrruptionen von Schneeeulen im Winter eine Strategie zur Aufrechterhaltung der Körperkondition sein könnten, wenn die Ressourcen im Brutgebiet aufgrund der großen Anzahl von Nachkommen, die im Laufe einer Brutsaison produziert werden, begrenzt werden.

Im zweiten Kapitel charakterisierte ich Nomadismus vs. reguläre Migration, zwei unterschiedliche Bewegungsmuster von Schneeeulen, und untersuchte mögliche Ursachen für diese zwei gegensätzlichen Bewegungsarten und ihre Konsequenzen für die Energieaufnahme. Die Studie zeigte, dass die unterschiedlichen Bewegungsmuster, die zwischen den Individuen gefunden wurden, eine Reaktion auf die unterschiedliche Ressourcenvariabilität sein könnten, die sie in ihrer Umwelt vorfinden, und dazu dienen, ein vergleichbares Niveau an Ressourcen, d.h. Potenzial für die Energieaufnahme, zu sichern.

Im dritten Kapitel untersuchte ich die Ursachen der Bewegung in Bezug auf die Ressourcenvariabilität und den Bruterfolg bei Raufußbussarden sowie die Bewegungsmuster in Bezug auf die Suche nach einem Nistplatz während der vorangegangenen Brutsaison. Die Ergebnisse legen nahe, dass Raufußbussarde den Zeitmangel kompensieren, indem sie den Nistplatz bereits während der vorherigen Brutsaison auswählen, und dass der Bruterfolg und die Ressourcenstabilität den Umfang der Prospektionsbewegung, d. h. der potenziellen Suche nach dem Nistplatz für das folgende Jahr, beeinflussen.

Im vierten Kapitel bewertete ich die Folgen von Bewegungsmustern, insbesondere unmittelbaren Reaktionen auf Umweltbedingungen bei drei arktischen Greifvogelarten. Die Studie zeigte, dass alle drei Arten dem nördlichen Verlauf der Schneeschmelze während des Frühjahrszuges folgten, was darauf hindeutet, dass sie die Schneeverhältnisse als Anhaltspunkt für den Zeitpunkt ihrer Ankunft in den Brutgebieten nutzen. Die Schneeeule und der Raufußbussard mit hoher Bewegungsflexibilität reagierten stärker auf die Schneeverhältnisse als der Wanderfalke mit weniger flexiblen Bewegungen.

Im fünften Kapitel schließlich untersuchte ich die vom Menschen herbeigeführten Ursachen der Bewegung als Folge der Anbringung von Tags an Tieren. Die Ergebnisse liefern den Beweis, dass die Tagging-Methode die Flugleistung bei südafrikanischen Kapgeiern beeinflusst und legen nahe, dass Patagial-Tags negative Auswirkungen auf die gefährdete Geierart haben. Dies ist sowohl für das Wohlergehen der Art als auch für die Qualität der gesammelten Daten von großer Bedeutung, die dadurch möglicherweise nicht repräsentativ sind und zu Fehlinterpretationen des beobachteten Verhaltens führen können.

Diese Erkenntnisse helfen uns nicht nur, die Bewegungsökologie von Tieren zu verstehen, sondern haben auch wichtige Implikationen für den Schutz der Art. Der nächste Schritt ist, weiter zu untersuchen, wie Individuen Information ihrer Umwelt verarbeiten und nutzen, da uns dieses Wissen helfen kann, die Auswirkungen zukünftiger Umweltveränderungen vorherzusagen. Wir werden in der Lage sein zu verstehen, wie Klimawandel Bewegungsentscheidungen auf kleiner Ebene beeinflusst, sowie Bewegungsmuster, die uns helfen würden, die Arten zu identifizieren, die Managementmaßnahmen benötigen.

General introduction

Animal movement

The movement of animals, from a small taxon as placozoa to an animal as large as the blue whale (*Balaenoptera musculus*), is a phenomenon that impacts entire ecosystems. One of the most fascinating types of movement is migration, usually a seasonal movement, where individuals or groups of individuals move to an area with more favourable environmental conditions for example in relation to weather and resources. Movement, even of larger vertebrates, can happen at different scales, from a sloth (suborder Folivora) covering no more than 38 meters daily to an arctic tern (*Sterna paradisaea*) that can cover 500 km in a day on its 30.000 km long migration. The motivation for moving can be foraging, searching for mates, reproduction, finding a shelter and/or avoiding predation. All these factors define the fate of an animal.

A movement path, that an animal undertakes, is determined by its internal state (Why to move?), its motion capacity (how to move?) and navigation capacity (Where to move?) all of which are influenced by external factors i.e. abiotic and biotic environmental conditions (Nathan et al. 2008). The internal state describes the physiological and/or psychological state of an individual that motivates movement. Motion capacity is determined by the biomechanical properties of an individual such as wings for moving through the air or fins for moving through the water. Finally, navigation capacity is the ability to detect information about the environment to successfully fulfil the task of moving between targets such as processing cues, retaining memory or the genetic basis for orientation and navigation.

The rapid development of tracking technologies allows us to record animals' positions at a high resolution which has significantly advanced our understanding of movement ecology. Tracking is mainly used to locate animals using the Global Positioning System (GPS), however, bio-logging sensors have been used to provide additional information on the animal's state and its environment (Kays et al. 2015a, Wilmers et al. 2015). Tracking devices and sensors can thus help us to investigate the causes, patterns and consequences of movement in animals.

Patterns of movement

Species, populations and individuals can exhibit different movement patterns, ranging from residency, dispersal, nomadism and regular migration (Newton 2012, Singh et al. 2012, Bastille-Rousseau et al. 2016). Residency is defined by the movements limited to the home-range area where individuals forage and reproduce. Dispersal is characterized by the relocation of individuals to another area without returning for example to breed. When an animal leaves a parental territory and dispersal occurs for the first time, the movement is termed natal dispersal, while subsequent changes in breeding sites are defined as breeding dispersal (Greenwood & Harvey 1982). Regular migration is identified by the often seasonal movements between the breeding and wintering area, high site fidelity and annual consistency in routes and timing. Nomadism, on the other hand, is defined by a low site fidelity and variable timing, distance and duration of the movement. A type of nomadism is irruptive migration where massive numbers of individuals move to the specific areas in some years but not in others (Newton 2008, Teitelbaum & Mueller 2019).

Animals can thus display regular movement from one year to another such as regular migration, or irregular movement such as nomadism, irruptions and switching between movement patterns. Some animals, however, exhibit mixed movement patterns that do not belong to a single category (Bunnfeld et al. 2011). This leads up to the question of what are the ecological and evolutionary drivers for such variation in movement patterns.

Causes of movement

Contrasting movement patterns are thought to evolve because of the different predictability of the environmental conditions animals are experiencing at different spatio-temporal scales (Riotte-Lambert & Matthiopoulos 2020). Specifically, the predictability of resources is considered as the main driver of movement patterns in the literature (Mueller & Fagan 2008, Bastille-Rousseau et al. 2017). Individuals experiencing low temporal predictability of resources are expected to be nomadic and individuals in areas with high temporal predictability should behave as residents or regular migrants (Mueller & Fagan 2008). At the spatial scale of resource distribution, coarse and clumped distribution should lead to regular migration, fine distribution promotes residency and nomadism arises at an intermediate distribution of resources (Mueller & Fagan 2008). Irruptive migration, however, occurs in

species specializing in resources that fluctuate in space and time (Newton 2006, 2008). For example, seed-eating birds rely on fluctuations in productivity of coniferous species (Larson & Bock 1986, Hochachka et al. 1999) and predatory birds specialize on fluctuations in number of small rodents (Sonerud 1997, Robillard et al. 2016). Dispersal can occur together with other movement patterns, regardless of the resource predictability. For example, an individual is resident in one area and disperses to another area in search for a mate or because of the resource-rich habitat. In the new area, the animal can either stay resident or move between the locations.

With spatio-temporal changes in resource distribution, some animals might be able to change between movement patterns from one season to the next. Moreover, biotic factors such as body condition, breeding success, and competition can cause differences in movement between one year and another (Barbraud et al. 2003, Kokko et al. 2004, Winkler et al. 2004). Movement patterns can be also affected by the human-induced causes such as supplementary feeding (Monsarrat et al. 2013), habitat and connectivity loss (Ramos et al. 2020), hunting pressure (Béchet et al. 2003), or effects of attached devices on animals (Barron et al. 2010, Bowlin et al. 2010, Bodey et al. 2018).

Consequences of movement

If different movement patterns evolved and co-existed within the same geographical area, there should be no difference in the consequences of movement patterns, such as the body condition, reproductive success or survival. Indeed, individuals with different movement patterns should strive towards a strategy that maximises their fitness and survival (Alerstam et al. 2003). However, trade-offs between different movement patterns exist and can be compensated for (Gillis et al. 2008, Grayson et al. 2011). Yet, some studies showed that resident birds had consistently higher fitness than migrants (Buchan et al. 2020).

Parallel with movement patterns, cognitive abilities developed as a response to environmental predictability where learning and memory developed in more predictable environments and information use in less predictable environments (Riotte-Lambert & Matthiopoulos 2020). Nomadic species thus have a higher proportion of flexible responses, such as information use from the environment, while migrants have a higher proportion of fixed responses, using learning and memory (Riotte-Lambert & Matthiopoulos 2020). It is thus expected that individuals with different movement patterns also should have different

proximate responses to environmental conditions. Individuals with flexible movement such as nomads, therefore, might gather information from the environment and use the environmental cues more than individuals exhibiting fixed movement, such as regular migrants.

In addition to movement patterns, also movement on a smaller spatio-temporal scale can affect fitness and survival of individuals. For example, a migratory individual that arrives early to the breeding grounds can access resource-rich territories and start breeding earlier which increases the probability of successful breeding (Bêty et al. 2003, Vergara et al. 2007). At the same time, the migration timing can be delayed due to the low body condition in the pre-migratory period (Cooper et al. 2015). These cause-effect relationships can help us understand animal movement.

Why arctic raptors?

In my PhD project, I used arctic raptor species as model organisms to investigate the patterns, causes and consequences of movement because as top predators of the Arctic they are especially affected by environmental change. These raptors generally move between the breeding areas in the Arctic and overwintering areas in lower latitudes. The breeding season in the Arctic is very short (Bêty et al. 2004, Madsen et al. 2007, Lamarre et al. 2017), thus the timing of arrival at the breeding grounds is crucial for successful breeding (Bêty et al. 2004, Madsen et al. 2007, Lamarre et al. 2017). While early arrival can secure territories for successful reproduction, being too early can expose migrants to harsh environmental conditions such as low temperature, snow cover, and scarcity of food. Additionally, food resources in the Arctic are highly fluctuating and arctic predators relying on small mammals as their main food source, must efficiently track or predict this variable resource. Arctic raptors should, during a very short season, closely track environmental conditions in order to arrive at the breeding grounds at the right time to find a suitable area for breeding. These tight connections between the environment and the animals' movement decisions make arctic raptors an interesting study species.

PhD project

The thesis is divided into the five chapters, each addressing specific research questions investigating the causes, patterns and consequences of movement. In the first four chapters, I used arctic raptor species as model organisms, while the fifth chapter is a study on an endangered vulture species that contributes knowledge on the impacts of attached devices on animal movement.

In the first chapter, I tested two alternative hypothesis to explain winter irruptions in snowy owls (*Bubo scandiacus*). According to the “lack-of-food” hypothesis, owls leave their regular wintering area because of the scarcity of food. Yet the “breeding output” hypothesis suggests that the irruption is a consequence of the high number of juveniles produced during years of high abundance of food who are leaving the natal area on dispersal. Following the “lack of food” hypothesis, irruptive owls are expected to be in suboptimal body condition and body condition should decrease with irruption intensity (concentrations of irruptive owls in areas they do not usually use for wintering). In accordance with the “breeding output” hypothesis, snowy owls should be in an optimal body condition because of the large food supplies available in the breeding grounds and this should be irrespective of irruption intensity. Previous studies have already assessed the body condition of snowy owls in regular wintering grounds of the Canadian Prairies and have noted that birds are generally in good body condition. However, the body condition of owls in highly variable or irregular winter areas such as northeastern North America or between years of different irruption intensity has never been studied.

In the second chapter, I assessed how resource variability shapes the movement patterns of individuals and identified the consequences in terms of resource use. I used the snowy owl as a study organism because it has highly flexible movement and is a diet specialist, meaning that the link between the habitat and food resources is strong. Differences in the temporal fluctuation of resources are expected to drive contrasting movement patterns i.e. nomadism and regular migration. However, empirical studies are needed to show how resource variability shapes contrasting movement patterns of individuals within the same geographical population and to identify the consequences of movement patterns in order to understand the adaptive advantages of different strategies. I hypothesized that individuals would prefer environments with low resource variability because they are more predictable. Since in some environments, the areas with highly variable resources are

more common than in others, some individuals would tend to move as regular migrants and others to move as nomads. As a consequence, the overall time spent in areas with different levels of resource variability and the resource use i.e. potential for energy intake would be comparable between the contrasting movement patterns.

In the third chapter, I looked into the movements of the rough-legged buzzard and investigated how breeding success and resource variability affect movement. Short summers and fluctuating resources in the Arctic make settlement decision for arctic breeders challenging. Rough-legged buzzards rely on rodent cycles, defined by a 3-5 year period where lemming and vole abundance is rising for a few years, reaching a peak and afterwards crashes. However, it remains unclear how arctic predators, especially migrants, are able to find the area with rodent peak in abundance during the very short settlement decision process. I hypothesised, that an individual that breeds successfully stays within the breeding area until the end of the breeding season, afterwards it migrates to the South to overwinter and in spring returns to the same location for breeding. An individual that fails to breed, however, leaves the breeding area and searches for a suitable breeding location for the following year. Following this phase of prospecting movement, it migrates to the wintering area and after spring migration, attempts to breed in the suitable breeding location that it found in the previous summer.

In the fourth chapter, I investigated whether species with contrasting movement patterns have different proximate responses to environmental conditions. Specifically, I focused on snow cover as an additional environmental factor that was rarely investigated before and might modulate spring migration movements. In arctic migrants, snow directly influences resource availability and presumably individual's movement decisions. Arctic migrants are expected to follow the spring snowmelt to optimise their arrival time to the breeding grounds. I compared the relationship between the spring movements and snow cover in three arctic predators with different movement patterns: the snowy owl is an irruptive species, peregrine falcon a regular migrant and rough-legged buzzard (*Buteo lagopus*) has a mixed movement pattern. The prediction was that the snowy owl would respond to the snow conditions the most, peregrine falcon (*Falco peregrinus*) the least, and the response of rough-legged buzzard would be between the two species.

In the fifth chapter, I focused on the human-induced causes for animal movement, specifically on the impacts of tagging methods on movement in an endangered species,

the Cape Vulture (*Gyps coprotheres*). The use of tracking technologies is key for the study of animal movement and pivotal to ecological and conservation research. However, the potential effects of devices attached to animals are sometimes neglected. The impact of tagging not only rises welfare concerns but can also biases the data collected, causing misinterpretation of the observed behaviour, which invalidates the comparability of information across individuals and populations. Patagial (i.e. wing) tags have been extensively used as a marking method for visual resightings in endangered vulture species, but their effect on the aerodynamics of the birds and their flight behaviour is yet to be investigated. In this study, I compared the impact of patagial tags vs leg bands in wild and captive-bred individuals on the flight performance, including flight probability, the proportion of time spent flying, cumulative distance travelled and ground speed.

Chapter 1

Winter irruptive Snowy Owls (Bubo scandiacus) in North America are not starving

Teja Curk, Tom McDonald, Dan Zazelenchuk, Scott Weidensaul, David Brinker, Steve Huy, Norman Smith, Trish Miller, Audrey Robillard, Gilles Gauthier, Nicolas Lecomte, Jean-François Therrien

Published in *Can. J. Zool.* 2018, **96**: 553-558

Abstract

Winter irruptions, defined as irregular massive movement of individuals over large distances, have been linked to food supply. Two hypotheses have been put forward: the “lack-of-food” suggests that a shortage of food forces individuals to leave their regular winter range, and the “breeding output” suggests that unusually large food supplies during the preceding breeding season allows production of a large number of offspring dispersing in winter. According to the breeding output hypothesis, irruptive snowy owls (*Bubo scandiacus* L., 1758) in eastern North America should not exhibit a lower body condition than individuals in regular wintering regions and individuals on the breeding grounds. Additionally, body condition of irruptive individuals should be unrelated to irruption intensity. Although body condition of juveniles was generally lower than that of adults and improved during the winter, we measured a fair body condition in both juvenile and adult irruptive snowy owls across North America. The results showed that snowy owls are not in a starving state during winter, and body condition of all age-classes was not related to winter irruption intensity. Those results support the breeding output hypothesis suggesting that winter irruptions seem to be primarily the result of a large number of offspring produced when food availability on the breeding grounds is high.

Introduction

Irruption migration, defined as irregular and massive movements of individuals associated with large fluctuations in food supplies, is one of the most dramatic migratory movements observed on land. This phenomenon produces huge concentrations of individuals in given years in some areas followed by a sharp reduction in numbers of individuals in other years at the same location. Irruption migration usually occurs in species specializing on pulsed resources (Newton 2006, 2008). Examples of irruptive migrants include seed eaters relying on mast fruiting events of a very limited number of coniferous species to reproduce (Larson & Bock 1986, Hochachka et al. 1999), and predatory birds (especially owls) specializing in one or more species of fluctuating small mammals (Sonerud 1997, Robillard et al. 2016).

Two hypotheses have been put forward to explain winter irruptions (Koenig & Knops 2001). The “lack-of-food” hypothesis suggests that a severe shortage of food forces individuals to move out of their regular range in search of food. Under such circumstances, most individuals are expected to be in a suboptimal body condition and/or in a starving state because the lack of food would have dramatically impacted food acquisition. This has been indeed shown in great grey owls (*Strix nebulosa*; Forster, 1772) during winter irruptions (Graves et al. 2012). Moreover, under this hypothesis, overall body condition should be negatively correlated with irruption intensity. In contrast, the alternate “breeding output” hypothesis suggests that winter irruptions occur when a very high food availability during the breeding season results in an unusually large number of offspring dispersing in winter (Koenig & Knops 2001). Under such scenario, these individuals should exhibit a good body condition in winter due to the large food sources available during the previous breeding season, and overall body condition should not be correlated with irruption intensity. The snowy owl (*Bubo scandiacus* L., 1758) is a top predator of the Arctic tundra and a typical example of an irruptive species. Indeed, during the summer it specializes on lemmings (*Dicrostonyx* and *Lemmus spp.*), which exhibit large amplitude fluctuations in abundance annually (Krebs et al. 2011). The snowy owl has a high reproductive potential and can benefit from lemming outbreaks by laying one of the largest clutches in birds of prey (up to 11 eggs, 76 mean = 7; Holt et al. (2015b)). During the winter season, the species can be regularly seen in the Canadian Prairies and American Great Plains but less so in eastern North America where it is present in large numbers only in irruptive years. It has long been thought that birds visiting irregular wintering areas were in a starving state, being forced out

of their regular range because of a lack of food resources (Shelford 1945, Chitty 1950, Lack et al. 1954, Newton 1970). Recent evidence, however, suggests that winter irruption of this species in North America can be explained by the breeding output hypothesis. Indeed, the winter abundance of snowy owls in temperate North America has been positively correlated to the previous summer density of lemmings on Arctic breeding grounds (Robillard et al. 2016). In addition, an apparent large proportion (>80%) of individuals observed in irruption years are juveniles (Smith 1997).

Previous studies have already assessed body condition of snowy owls in regular wintering grounds of the Canadian Prairies and have noted that birds are generally in good body condition (Kerlinger & Lein 1988, Chang & Wiebe 2016). However, body condition of owls has never been studied in highly variable or irregular winter areas such as northeastern North America or between years of different irruption intensity. We hypothesized, according to the breeding output hypothesis, that irruptive snowy owls outside of their regular winter range should not be in a starving state, just like on regular wintering grounds, and that the body condition should be unaffected by irruption intensity.

Methods

Study areas and field data

Consistently between 1 October and 30 April each year from 1991 to 2016, live snowy owls were routinely trapped using bow-net and bal-chatri traps and banded in several areas of the species' winter distribution in North America. This included regular (Saskatchewan and Alberta) and highly variable or irregular (Delaware, Maryland, Minnesota, New York, Pennsylvania, and southern Québec) winter areas, and as part of concomitant research projects on their breeding grounds in northern Québec and Nunavut. Periods during which owls were trapped did not differ between the regular and irregular wintering areas. We recorded the age and sex of each individual according to plumage characteristics following (Josephson 1980, Seidensticker et al. 2011, Solheim 2012). Because snowy owls start molting their flight feathers when they reach one year of age (Solheim 2012), individuals were identified as juveniles (less than 12 months of age) if they still wore their juvenile feathers and had not molted any flight feathers; otherwise, individuals were considered

adults. This classification resulted in four age-sex classes (juvenile female, juvenile male, adult female and adult male). For each individual, we recorded body mass (± 10 g) using PESOLA spring scales or electronic balances and wing chord (± 1 mm) using rulers. All bird-banders used a standardized technique to measure unflattened wing chord. However the wing chord measurements differed between the banders on average for 4.7 ± 6.1 mm for females and 12.2 ± 9.0 mm for males (LM: $p < 0.001$, $n = 566$ for females and $p < 0.001$, $n = 462$ for males), therefore bander ID was used as a random variable in the analyses.

During one winter (2013 - 2014), we also collected breast muscle samples on a limited number of snowy owl carcasses brought to us following airplane or vehicle collisions in irregular wintering areas. We sampled only individuals that were killed instantly by the strike and were kept frozen until sampled. We used those samples to assess the percentage of fat in muscles and the carbon/nitrogen (C/N) ratio, an additional proxy for lipid content (Ehrich et al. 2011). Muscle samples (about 1g) were freeze-dried at -50°C for 72 hours and then ground to a fine powder with mortar and pestle. Lipids were extracted with pure chloroform using a Soxhlet apparatus (Tecator system 1043) and measured as a percentage of sample mass. C/N ratios were determined from percentage element weight measured by mass spectrometry conducted during concomitant stable isotope analyses (see Robillard et al. (2017) for details).

To assess annual winter irruption intensity, we used Christmas Bird Count (CBC) data (National Audubon Society 2010), a well-known citizen-science database gathering annual birding records of thousands of volunteers made during a single day between December 14 and January 5 across North America. The surveys include the number of hours spent in the field per party (i.e., a group of persons counting birds together), and observer effort is thus calculated in party-hr. We used the number of snowy owls reported per party-hr from 1991 to 2015 across northeastern North America using the states and provinces where snowy owls are irregular winter visitors (Connecticut, Delaware, Maine, Maryland, Massachusetts, Michigan, Minnesota, New Brunswick, New Hampshire, New Jersey, New York, Nova Scotia, Ohio, Ontario, Pennsylvania, Québec, Rhode Island, Vermont, and Wisconsin).

Body condition indices

We estimated body condition indices separately for males and females because snowy owls exhibit a strong sexual dimorphism (Holt et al. 2015*b*). We corrected body mass for body size using ordinary least squares (OLS) residuals obtained by regressing body mass on wing chord (Labocha & Hayes 2012). The residuals represent positive or negative deviations of body mass values predicted by wing chord where positive residual values represent heavier individuals (assumed in better condition) and negative values represent lighter individuals (assumed in worse condition) than predicted. With this method, residuals of body mass are not correlated with the predictor variable (wing chord) and estimated body condition is therefore not dependent or changeable with body size.

Statistical analysis

First, we assessed whether body condition of male and female snowy owls tended to improve during the winter season separately in regular and irregular areas using linear mixed models (LMM's). We performed a separate model for each sex and used OLS residuals as dependent variable, day (day of the winter season from 1 October to 1 April) and age class as fixed effects, and winter season, study area (categorical variable containing nine locations where data were collected), and bander ID as random effects. Because body condition tended to improve during the winter (see Results), we only used owls measured early in the winter season (before January 1) in all following analyses, unless specified.

Second, we tested the difference in body condition between irregular and regular wintering areas using linear mixed models (LMM's). Separate models for males and females were carried out using OLS residuals as a dependent variable, region (regular vs irregular wintering areas) and age class as fixed effects, and winter season (categorical variable where each level represents one winter from 1991/1992 to 2015/2016) and bander ID as random effects.

Third, we measured whether body condition of snowy owls was linked to irruption intensity in irregular wintering areas using linear models (LM's). We run a separate model for each sex and used OLS residuals as a dependent variable and CBC value, and age class as fixed effects.

Fourth, to assess whether body condition of adult females at irregular wintering areas

differs from that of breeding females, we fitted a LMM with OLS residuals as dependent variable, period (breeding vs wintering) as fixed effect and season (categorical variable where each level represents a winter from 1991/1992 to 2015/2016 or a breeding season from 2007 to 2014), and bander ID as random effects.

Models were ranked according to the Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Model averaged estimates and their 95% confidence intervals were computed with multi-model inference on the best models (i.e. $\Delta AIC < 2$) using the AICcmodavg package (Mazerolle et al. 2016). All statistical analyses were performed using R version 3.2.1. (R Development Core Team 2015) and the package lme4 (Bates et al. 2015).

Results

Body condition of snowy owls was lower in juveniles than adults and generally improved over time both in regular and irregular wintering areas, especially in juveniles (Table 1.1, Figure 1.1, Table S1.1). In regular wintering areas, juvenile females increased their body condition index by 132.1 g per month ($n = 88$), whereas the increase was more modest in irregular wintering areas (30.8 g per month, $n = 188$). Adult females in irregular wintering areas increased their body condition index by 14.8 g per month ($n = 88$) and juvenile males by 29.3 g per month ($n = 213$) in the same areas.

In accordance with our main prediction that wintering snowy owls would not be in a starving state in irregular wintering areas, the measured index of body condition was actually better in irregular wintering areas compared to regular ones for most age-sex classes (adult females in regular areas: 116.9 ± 13.8 g, $n = 186$; adult females in irregular areas: 21.9 ± 18.7 g, $n = 120$; adult males in regular areas: 22.4 ± 23.3 g, $n = 102$; adult males in irregular areas: 57.8 ± 22.6 g, $n = 65$; juvenile females in regular areas: -215.3 ± 19.6 g, $n = 89$; juvenile females in irregular areas: -35.3 ± 15.5 g, $n = 189$; juvenile males in regular areas: -55.5 ± 15.1 g, $n = 81$; juvenile males in irregular areas: -1.3 ± 9.8 g, $n = 214$; Table 1.2, Figure 1.2, Table S1.2).

Irruption intensity (CBC value) was not related with overall body condition of wintering male and female snowy owls captured early in winter in irregular wintering areas (Table 1.3, Table S1.3).

Body condition of adult females was slightly higher in individuals captured during the breeding season than individuals captured early during the winter in irregular areas (breeding season: 97.1 ± 32.3 g, $n = 19$; early in winter season: 12.2 ± 24.8 g, $n = 35$, Table 1.4, Figure 1.3, Table S1.4). The overall body condition index was nonetheless positive for adult females in irregular wintering areas suggesting an overall fair body condition despite the difference with breeding birds.

Average ($\pm$ SE) body mass of individuals sampled early in winter in irregular areas was $2,086.8 \pm 25.4$ g ($n = 37$) and $1,571.7 \pm 28.4$ g ($n = 23$) for adult females and males respectively, and $2,027.8 \pm 19.3$ g ($n = 113$) and $1,534.3 \pm 18.5$ g ($n = 104$) for juvenile females and males, respectively. Considering that body masses of emaciated snowy owls during the winter season were established at around $1,286 \pm 66$ g for females and 975 ± 26 g for males (Chang & Wiebe 2016), all individuals from the present study were well above those thresholds. Overall, only four (2%) juvenile females (body mass $< 1,400$ g) and six (3%) juvenile males (body mass $< 1,100$ g) were approaching the emaciated threshold in the irregular wintering areas.

The average percentage of fat measured in muscles was high (15.0%, SD = 12.9%, $n = 24$). In addition, C/N ratios obtained from the same muscle samples also suggest a rather good body condition (average = 3.5, SD = 0.2, $n = 24$; Tarroux et al. (2010)).

Discussion

Overall, winter irruptive snowy owls captured in northeastern North America generally displayed a good body condition, with fewer than 2% of the measured individuals approaching the emaciated threshold. Those results are in agreement with previous studies conducted in regular snowy owl wintering areas such as the Canadian Prairies (Kerlinger & Lein 1988, Chang & Wiebe 2016). Those results are also consistent with our prediction that snowy owls are not in poor body condition or starving state when they irrupt in northeastern

Table 1.1. Model selection explaining body condition index (OLS residuals) of snowy owls (*Bubo scandiacus* L., 1758) according to day (day of the winter season from 1 October to 1 April) tested separately by sexes in regular (North America Prairies) and irregular (northeastern North America) wintering areas, using linear mixed models fitted with maximum likelihood. The best selected models where Δ AIC is less than 2 are presented in bold.

Response variable: Residuals	Predictor variables	K	Δ AIC	AIC Weight	Log-likelihood
Change in body condition of female snowy owls throughout winter in regular wintering areas (n = 275)	Day * Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	8	0.0	0.6	-1842.4
	Day + Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	7	0.5	0.5	-1843.7
	Day + (1 Winter season) + (1 Study area) + (1 Bander ID)	6	80.4	0.0	-1884.6
	Null + (1 Winter season) + (1 Study area) + (1 Bander ID)	5	81.3	0.0	-1886.1
	Day * Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	7	0.0	0.6	-1178.4
Change in body condition of male snowy owls throughout winter in regular wintering areas (n = 138)	Day * Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	8	0.4	0.5	-1177.6
	Null + (1 Winter season) + (1 Study area) + (1 Bander ID)	5	35.0	0.0	-1198.0
	Day + (1 Winter season) + (1 Study area) + (1 Bander ID)	6	36.0	0.0	-1197.4
	Day + (1 Winter season) + (1 Study area) + (1 Bander ID)	6	0.0	0.6	-1801.3
Change in body condition of female snowy owls throughout winter in irregular wintering areas (n = 275)	Day * Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	8	1.6	0.3	-1800.1
	Day + Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	7	2.0	0.2	-1801.3
	Null + (1 Winter season) + (1 Study area) + (1 Bander ID)	5	17.0	0.0	-1810.8
	Day + Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	7	0.0	0.6	-1802.1
Change in body condition of male snowy owls throughout winter in irregular wintering areas (n = 278)	Day * Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	8	1.4	0.3	-1801.9
	Day + (1 Winter season) + (1 Study area) + (1 Bander ID)	6	4.9	0.1	-1805.6
	Null + (1 Winter season) + (1 Study area) + (1 Bander ID)	5	25.8	0.0	-1817.1
	Day + Age class + (1 Winter season) + (1 Study area) + (1 Bander ID)	7	0.0	0.6	-1802.1

*Winter season is a categorical variable where each level represents one winter from 1991/1992 to 2015/2016; Study area is a categorical variable containing nine locations where data were collected; Bander ID is a categorical variable including 11 levels where each level represents a name of the bander; Age class in a categorical variable which includes two levels (adult and juvenile).

Table 1.2. Model selection explaining body condition index (OLS residuals) of snowy owls (*Bubo scandiacus* L., 1758) according to region (regular vs irregular wintering areas) tested separately by sexes using linear mixed models fitted with maximum likelihood. The best selected models where Δ AIC is less than 2 are presented in bold.

Response variable: Residuals	Predictor variables	K	Δ AIC	AIC Weight	Log-likelihood
Difference in body condition of female snowy owls between irregular and regular wintering areas (n = 261)	Region * Age class + (1 Winter season) + (1 Bander)	7	0.0	1	-1740.2
	Region + Age class + (1 Winter season) + (1 Bander)	6	23.4	0	-1753.0
	Region + (1 Winter season) + (1 Bander)	5	61.6	0	-1773.1
	Null + (1 Winter season) + (1 Bander)	4	66.1	0	-1777.3
	Region * Age class + (1 Winter season) + (1 Bander)	7	0.0	0.9	-1346.6
Difference in body condition of male snowy owls between irregular and regular wintering areas (n = 206)	Region + Age class + (1 Winter season) + (1 Bander)	6	3.5	0.2	-1349.3
	Null + (1 Winter season) + (1 Bander)	4	18.4	0.0	-1359.8
	Region + (1 Winter season) + (1 Bander)	5	21.7	0.0	-1359.4
	Region * Age class + (1 Winter season) + (1 Bander)	7	0.0	0.9	-1346.6

*Winter season is a categorical variable where each level represents one winter from 1991/1992 to 2015/2016; Bander ID is a categorical variable including 11 levels where each level represents a name of the bander; Age class in a categorical variable which includes two levels (adult and juvenile).

Table 1.3. Model selection explaining body condition index (OLS residuals) of snowy owls (*Bubo scandiacus* L., 1758) according to winter irruption intensity (i.e. Christmas Bird Count [CBC] value given for each winter season) tested separately by sexes using linear models fitted with maximum likelihood. The best selected models where Δ AIC is less than 2 are presented in bold.

Response variable: Residuals	Predictor variables	K	Δ AIC	AIC Weight	Log-likelihood
Effect of irruption intensity on body condition of female snowy owls early in the winter in irregular wintering areas (n = 144)	Null	2	0.0	0.4	-972.9
	CBC + Age class	4	0.3	0.3	-971.0
	CBC	3	1.3	0.2	-972.6
	CBC * Age class	5	2.3	0.1	-971.0
	Null	2	0.0	0.4	-840.4
Effect of irruption intensity on body condition of male snowy owls early in the winter in irregular wintering areas (n = 127)	CBC * Age class	5	0.3	0.3	-837.5
	CBC	3	1.5	0.2	-840.1
	CBC + Age class	4	2.1	0.1	-839.4
	Null	2	0.0	0.4	-840.4

*Age class in a categorical variable which includes two levels (adult and juvenile).

Table 1.4. Model selection explaining body condition index (OLS residuals) of snowy owls (*Bubo scandiacus* L., 1758) according to period (breeding vs wintering) tested for adult females using linear mixed models fitted with maximum likelihood. The best selected models where Δ AIC is less than 2 are presented in bold.

Response variable: Residuals	Predictor variables	K	Δ AIC	AIC Weight	Log-likelihood
Difference in body condition of adult females between breeding season and early in winter in irregular wintering areas (n = 55)	Period + (1 Season) + (1 Bander ID)	5	0.0	0.3	-350.7
	Null + (1 Season) + (1 Bander ID)	4	2.1	0.1	-352.7

*Season is a categorical variable where each level represents a winter from 1991/1992 to 2015/2016 or breeding season from 2007 to 2014; 26 Bander ID is a categorical variable including 11 levels where each level represents a name of the bander.

North America during winter. Juveniles of both sexes showed on average lower body condition values than adults, which suggests that this age class has an overall lower body condition, especially early in the winter season. This is not surprising since juveniles lose mass after fledgling to develop stronger muscles and bones and only start gaining fat later. In addition, juveniles are expected to be less dominant (Chang & Wiebe 2016), and therefore might have lower access to food than the adults. Juveniles nonetheless improved their body condition throughout the winter season and actually reached a level similar to adults while body condition of adults remained mostly unchanged throughout the winter

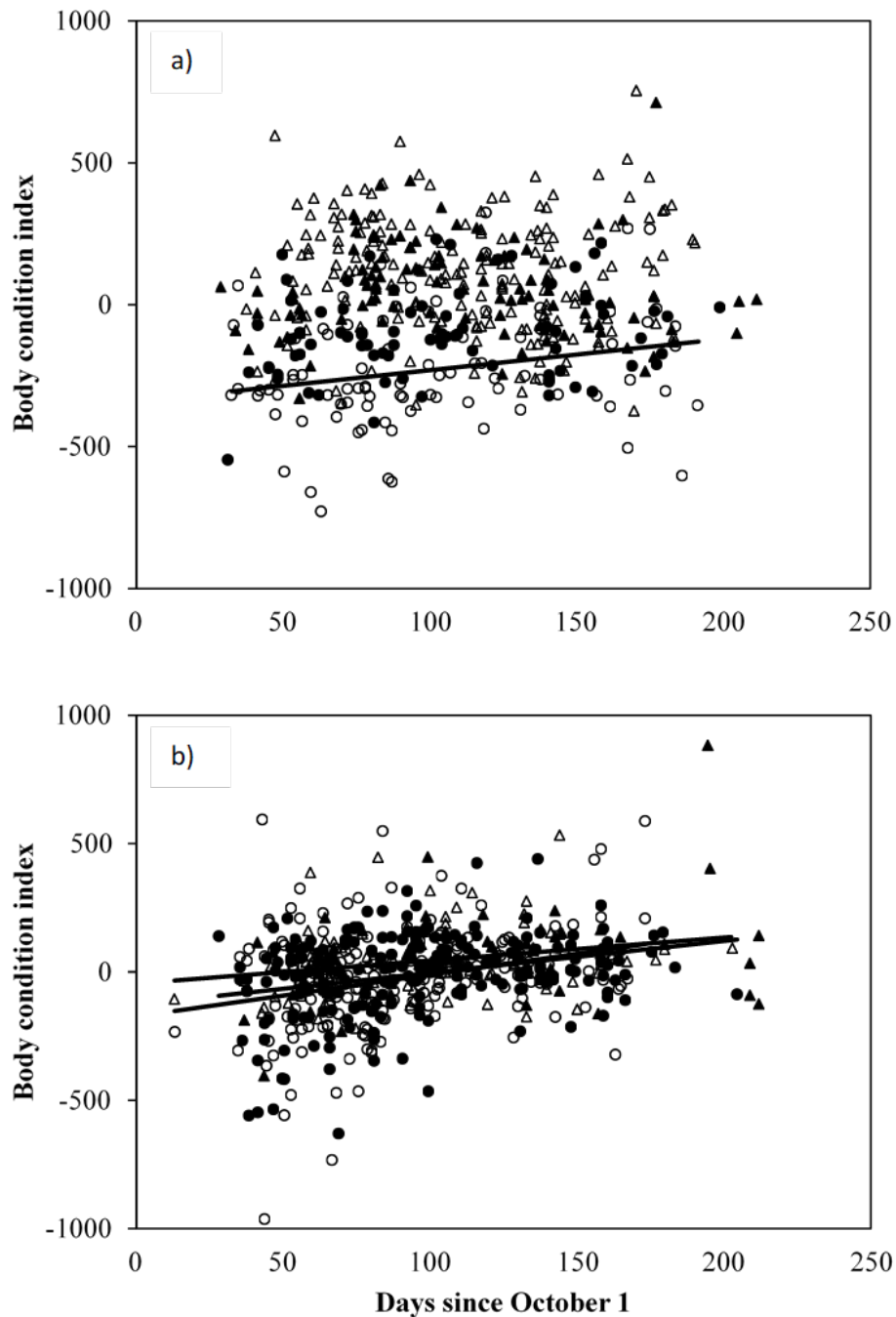


Figure 1.1. Body condition index (OLS residuals) of snowy owls (*Bubo scandiacus* L., 1758) captured during the winter season in a) regular wintering areas (North America Prairies) and b) irregular wintering areas (northeastern North America) in relation with time since October 1. Juvenile individuals are illustrated with circles and adults with triangles. Females are represented with open symbols and males with solid ones. Only significant slopes are presented. Slope in a) represents juvenile females, top slope in b) represents juvenile female, middle adult male, and bottom adult female.

season. The improvement of body condition throughout the winter season was seen in both

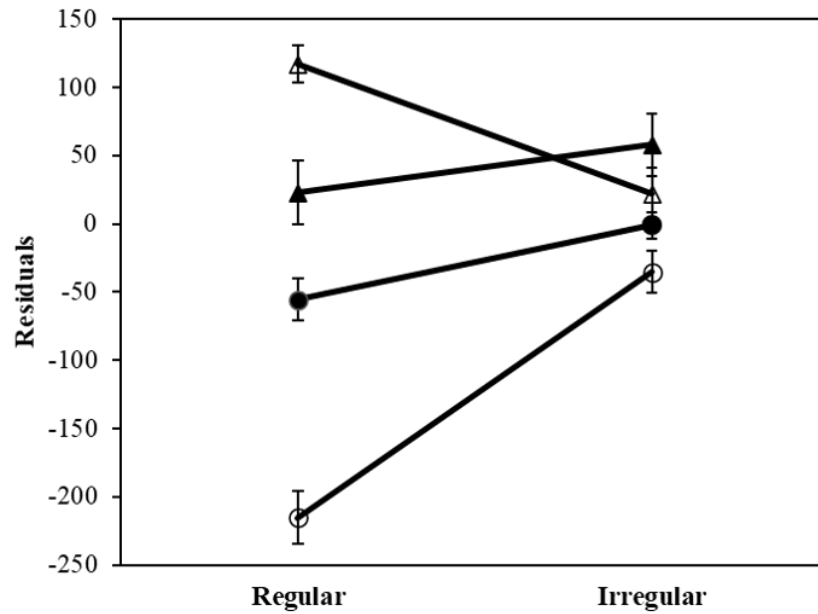


Figure 1.2. Mean $\pm$ SE of body condition index (OLS residuals) of snowy owls (*Bubo scandiacus* L., 1758) captured during the non-breeding season in regular (North America Prairies) and irregular wintering areas (northeastern North America). Adult females are represented with diamonds, adult males with squares, juvenile females with triangles, and juvenile males with crosses.

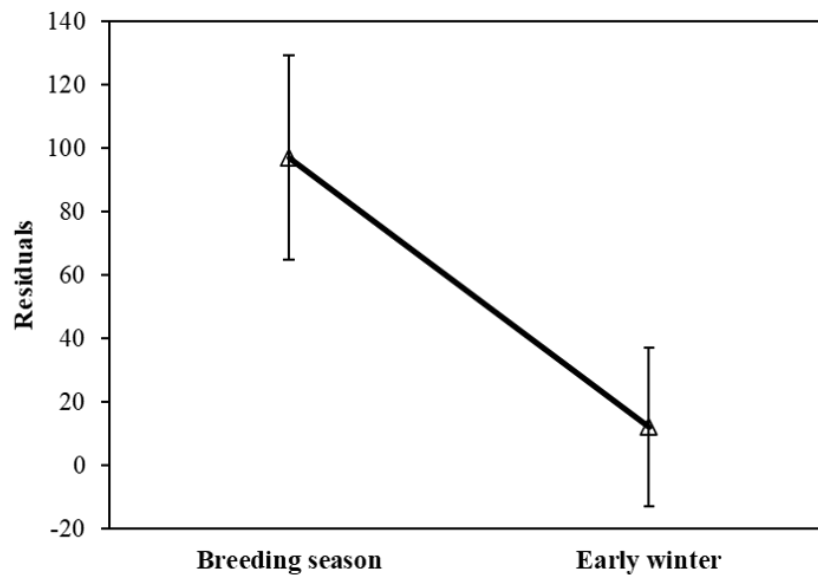


Figure 1.3. Mean $\pm$ SE of body condition index (OLS residuals) of adult female snowy owls (*Bubo scandiacus* L., 1758) captured in irregular wintering areas (eastern North America) during the breeding season and early in winter (before January 1).

regular and irregular wintering areas. Nonetheless, body condition was generally better in irregular than in regular wintering areas. This may be explained by the fact that individuals irrupting in irregular areas do so mostly following periods of high resource availability on the breeding grounds whereas individuals come in regular winter areas following years of both high and low resource availability.

We detected a lower body condition in adult females early in the winter season compared to breeding females. However, none of the individuals approached the emaciated threshold. Breeding individuals are probably those exhibiting the best body condition overall and so we believe that the detected difference should not be interpreted as being a sign of poor body condition during winter in irregular areas. Breeding females were captured in years when food was locally abundant (i.e. high lemming years) and toward the end of the incubation period when they are fed by adult males and food requirements of chicks is minimal. Therefore, it is not surprising that the body condition of these individuals tended to be higher than in early winter.

Our results suggest a good body condition overall for winter irruptive snowy owls and apparently very few starving and/or emaciated individuals. This is in agreement with the “breeding output” hypothesis (Koenig & Knops 2001), which suggests that a large number of juveniles produced during the breeding season when lemming abundance peaks would lead to winter irruptions (Robillard et al. 2016). A similar situation is to be expected in other mobile species relying on pulse resources for breeding such as seed eating birds (e.g. crossbills, siskins) as well as several owl species, but especially for those who have the capacity to lay large clutches. Indeed, during years of high food availability, average clutch size of both the snowy owl and the northern hawk owl (*Surnia ulula* L., 1758) is around eggs (and up to 11 and 13 respectively; Holt et al. (2015b), Duncan & Duncan (1998)). Those two species are thought to irrupt in winter following the “breeding output” hypothesis. In contrast, the great grey owl, which is a close cousin of the snowy owl and also specializes on small mammals during breeding has an average clutch size of 4.6 (up to 5) in good food years (Bull & Duncan 1993). This species is thought to irrupt following the “lack-of-food” hypothesis and body condition recorded in this species in winter supports this assumption (Graves et al. 2012). Whether clutch size is a predictor of the drivers behind irruptive strategies remains to be tested yet limited empirical data on body condition during winter irruption exist for other owl species and seed eating birds (but see Korner-Nievergelt

et al. (2008)).

Irruption migration might be a strategy to maintain body condition when resource-rich habitats on the breeding grounds become limited due to the large number of individuals. Indeed, small mammal abundance in peak years often decreases during the summer in response to high predation intensity (Fauteux et al. 2015) and thus food resources may actually become limited during autumn, especially for subordinate juveniles (Chang & Wiebe 2016). Although the breeding output hypothesis may encapsulate the mechanisms behind winter irruptions in several irruptive species such as the snowy owl, a decrease in food abundance per capita in late summer may also drive large number of young to overwinter in temperate regions, so both hypotheses may not be mutually exclusive.

Acknowledgements

We are thankful to all Project SNOWstorm (www.projectsnowstorm.org) supporters and colleagues, especially M. Blom, M. Lanzone and A. McGann. We acknowledge the support of the Natural Science and Engineering Research Council of Canada and the Canada Research Chair program. This is Hawk Mountain Sanctuary contribution to conservation science number 289 and Project SNOWstorm contribution 002.

Chapter 2

Contrasting movement patterns are the snowy owls' response to difference in resource variability

Teja Curk, Ivan Pokrovsky, Nicolas Lecomte, Tomas Aarvak, Kirk Bates, David F. Brinker, Mark Fuller, Gilles Gauthier, Karl-Otto Jacobsen, Olga Kulikova, Ingar J. Øien, Norman Smith, Roar Solheim, Scott Weidensaul, Karen Wiebe, Martin Wikelski, Jean-François Therrien, Kamran Safi

In preparation

Abstract

Background

Regular migration is characterized by high site fidelity and annual consistency in routes and timing while nomadism typically is defined by low site fidelity and variable timing as well as distance and duration when moving large distances. Low resource variability is expected to favour regular migration while high variability is being linked to nomadism. How precisely resource variability shapes the contrasting movement patterns at an individual level within the same population and the consequences thereof are key to understand the adaptive advantages of these emergent different strategies. Here, we investigate whether snowy owls which exhibit these contrasting movement patterns do so in response to the temporal predictability of resources and whether the consequences on resource use are comparable between individuals exhibiting contrasting movement patterns.

Methods

Using position information, we quantified movement patterns, from the tendency for nomadism to regular migration in a continuous variable and calculated utilization distribution (UD) of annual trajectories. By annotating NDVI (Normalized Difference Vegetation Index) to the UD rasters we estimated resource variability and use. First, based on NDVI values over the last two decades we quantified intra- and inter-annual variability, which we used as a proxy for resource variability. Second, based on the NDVI values matching the time of the tracking data we estimated resource use within the UD. Finally, we compared resource variability and use to the different movement patterns.

Results

Our study shows that, as expected, with lower resource variability snowy owls were more likely to move as regular migrants. However, irrespective of where on the regular migration to nomadism continuum an individual was, resource use and thus energy intake was found to be at similar levels.

Conclusions

Our study demonstrates that resource variability underlies the contrasting movement patterns exhibited by the snowy owl. The different movement patterns yet yielded the same benefits in terms of resource availability and use. Our study thus suggests that the contrasting movement patterns might overall provide the same adaptive outcome.

These findings are important for understanding the evolution and ecological mechanisms underlying animal movement strategies. Our findings are also important for the conservation of the species. With global change inducing more environmental unpredictability, we expect that nomadism will provide a rapid response to the changing conditions and replace regular migration as a large distance movement strategy with reductions in population density due to the larger space use requirements associated with nomadism.

Background

Investigating the causes and consequences of movement is of great importance for understanding the evolution, ecology, and behaviour of animals, especially in an anthropogenically induced rapidly changing environment (Nathan et al. 2008). Regular migration and residency are considered the end points of a continuum of movement patterns, with nomadism in between. Individuals, populations and species can exhibit movement patterns anywhere along this continuum (Cagnacci et al. 2011, Bastille-Rousseau et al. 2016, 2017). Regular migrants are characterized by high site fidelity and their annual consistency in routes and timing, nomads with low site fidelity and variable timing, distance and duration of migration, and residents with movements restricted to one or very few specific areas (Newton 2012, Singh et al. 2012, Bastille-Rousseau et al. 2016). Environmental predictability and the spatio-temporal scale of resource distribution is thought to underlie these movement patterns (Riotte-Lambert & Matthiopoulos 2020). While regular migration and residency are the two end points on a spatial scale of resource availability, from clumped to evenly distributed, nomadism and regular migration represent the end points on a temporal scale, from low to high resource predictability (Mueller & Fagan 2008, Singh et al. 2012).

Several species with a wide geographical range such as the European roe deer (*Capreolus capreolus*) and moose (*Alces alces*) show a latitudinal gradient in movement patterns where the populations in the North are regular migrants and those in the South are residents (Cagnacci et al. 2011, Singh et al. 2012). Similarly, partial migration, where part of the population is migratory and part is resident, is common among animal species (Chapman et al. 2011). However, studies of the same species within the same contiguous population, showing contrasting movement patterns such as nomadism and regular migration, are lacking. In addition, movement patterns are often categorized into discrete classes of regular migration, residency, nomadism and dispersal with intermediate movement patterns rarely being considered. A study by Bastille et al. (Bastille-Rousseau et al. 2017) on Galapagos giant tortoises (*Chelonoidis spp.*) made a step forward by linking environmental predictability to movement patterns. Yet, more studies showing empirical evidence that animals exhibit movement patterns as a response to environmental predictability are needed to understand how movement patterns evolved across animal taxa. Furthermore, the consequences of movement patterns need to be identified in order to understand the adaptive advantages of different strategies. Indeed, populations and individuals are expected to strive towards a

strategy that maximises energy intake and thus their fitness and survival (Alerstam et al. 2003).

In this study, we investigate within-species differences in movement patterns in the snowy owl (*Bubo scandiacus*), an ideal model organism because it exhibits a range of movement patterns (from nomadism to migration). The snowy owl is a top predator in the arctic ecosystem and not being predated itself, it is only the environment as such and the availability of prey that drives its movements (Alerstam et al. 2003, Blake et al. 2013). Finally, with the snowy owl being a dietary specialist the link between habitat and food resources is tight and comparable between populations, locations and years (Kerlinger et al. 1985, Therrien et al. 2014, Chang & Wiebe 2016). Based on movement data of snowy owls, we investigated whether the snowy owls' movement patterns are a response to (i) the different resource variability i.e. temporal predictability of resources they are experiencing, (ii) the overall resource variability and (iii) whether the overall resource use i.e. potential for energy intake is comparable between individuals exhibiting different movement patterns.

We hypothesize that the temporal fluctuation of resources, drives movement patterns in the snowy owls (Figure 2.1). We also hypothesize that the co-existence of the different movement patterns in the snowy owl represents stable strategies maximizing their fitness and survival, regardless of the differences in resource availability in the areas they occupied. Therefore, resource use would not differ between the individuals exhibiting contrasting movement patterns.

Methods

Tracking data

We obtained snowy owl GPS and Argos tracking data across North America and Eurasia (for details on permits, trapping locations and methods see Curk et al. (2020)). We removed duplicated timestamps, and filtered outliers based on speed ($>22\text{m/s}$) for GPS data, using the "ctmm" R package (Calabrese et al. 2016) and based on Freitas et al. (2008) algorithm for Argos data, using the "argosfilter" R package (Freitas 2010).

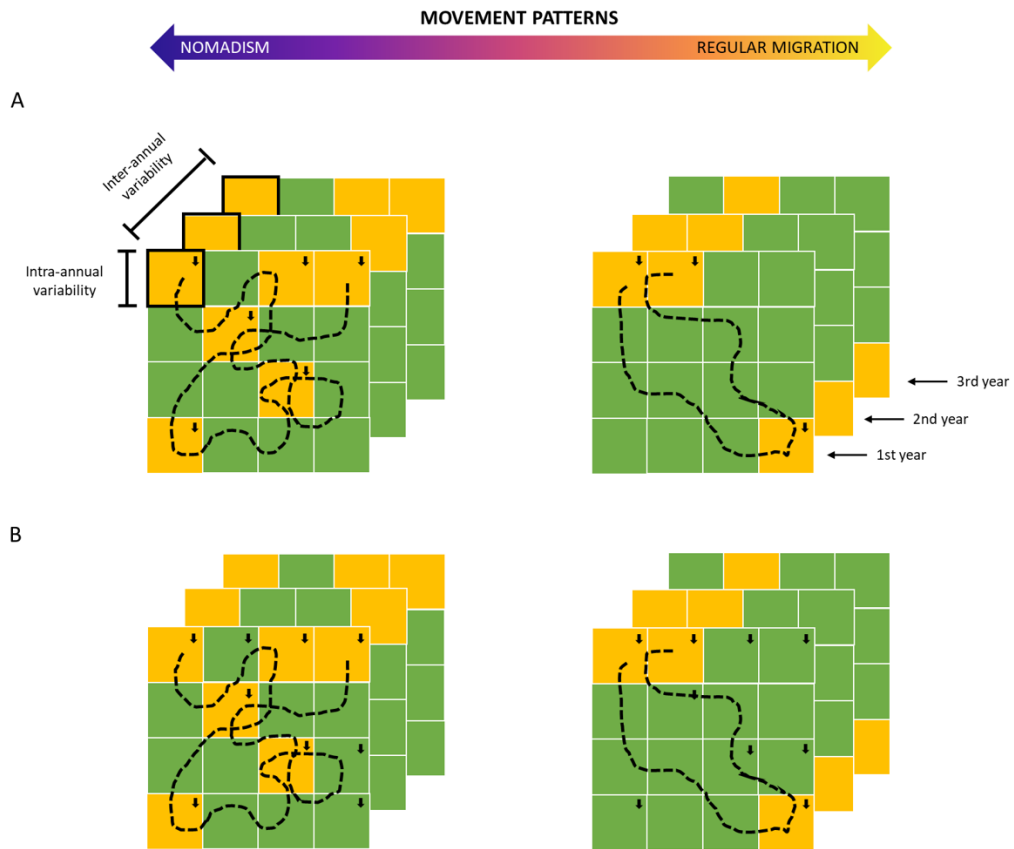


Figure 2.1. We hypothesize that the resource variability would drive movement patterns in snowy owls. Resource variability consists of changes in resource availability between the months of the same year (intra-annual variability) and between different years (inter-annual variability) at the same spatial area (square with a black frame). Orange squares represent areas where an individual spent more time and green squares areas where an individual spent less time. Individuals should generally avoid environments with high resource variability because of their unpredictability and thus spend a higher proportion of time in areas with low variability (black arrows). Note that the cells without an arrow, represent high resource variability. (A) When two individuals experience environments with a different distribution of areas of low and high resource variability, their movements (nomadic vs migratory) would be a consequence of their preference for low resource variability. (B) When two individuals experience environments with the same distribution of areas of low and high resource variability, the difference in their movements (nomadic vs migratory) would be due to the different choice of areas with low resource variability. In both cases, A and B, individuals show some degree of consistency in movement pattern between years because they prefer low variability of resources, however, because they chose among alternative low-variability areas, they can show differences in movement between years. As a consequence for this preference for low resource variability, the overall time spent in areas with different levels of resource variability would be comparable between individuals exhibiting contrasting movement patterns.

From Argos data, we also removed classes lower than one, such that location accuracy was <1000m. For the purpose of determining movement patterns, we used July 1st (middle of the breeding season) as the first location in the annual trajectory of individuals and used only tracks that covered more than 350 days of data. Since sampling intervals were not consistent across data collected at different field sites, we thinned movement data to 6h using the "move" R package (Kranstauber et al. 2013). After data cleaning, the data set consisted of 39 individuals and 55 annual trajectories, covering the years between 2001 and 2019.

Movement patterns

For the determination of movement patterns, we used a Movement Pattern Metric (MPM), which measures a tendency for migration and nomadism from an individual annual track. It is a continuous variable where 0 represents full nomadism and 1 fully regular migration. MPM is an extension of the classification method by (Bunnefeld et al. 2011) which is based on the Net Squared Displacement (NSD). NSD measures a distance from the starting location to all subsequent locations in the annual track of the individual. Plotted NSD values against time, thus result in contrasting shapes for the different movement patterns (Figure S2.1 D-F). We calculated NSD using July 1st as a starting date and used only tracks without major gaps between locations (<2 months) to not impair the correct determination of movement patterns.

As the first criterion, we ran non-linear regression models (nls) on NSD vs. time values as described in (Bunnefeld et al. 2011) using adjusted parameters for the timing and distance of migration. For each trajectory, we used two nls models, one for migration and one for nomadism since we did not have any sedentary or dispersing individuals present in our study. The migration model is a repeated double-sigmoid function representing a departure from the breeding area, migration, wintering and returning to the same location at the breeding area. For the migration model, we used the following initial parameter values: 3000 for the asymptotic height, 105 and 285 for the timing at which the migration reaches half its asymptotic height in spring and autumn, respectively, 5 for the time passed between reaching half and three quarters of spring and autumn migration, and Julian date as the number of days since July 1. The model for nomadism is a linear function where the distance from the original point increases through time. An individual migrates and finds

a new breeding area far away from the original location. For this model we used: Julian date as a number of days since July 1st and a constant slope of 20 without an intercept. From each nls model, we calculated quasi- R^2 value (Spiess & Neumeyer 2010) which is a measure of how well the function fit the data. We thus obtained two values of goodness of fit (R^{2_m} - for migration, and R^{2_n} for nomadism) from which we calculated a continuous measure where values close to zero represent nomadism and values close to one represent migration:

$$R = \frac{R^{2_m} + (1 - R^{2_n})}{2}$$

As a second criterion, we used normalized NSD difference between the first and last NSD value (*dist*) to re-scale the variable to 0 - 1. A larger value means that an individual has a tendency for nomadism and a smaller value, the tendency for migration. The equation is thus:

$$D = 1 - dist$$

As a third criterion, we included the difference between the max NSD values in winter (Feb-Mar) ($p1$) and summer (Jun-Jul) ($p2$) to identify whether the NSD values in summer were higher or lower than in winter. For nomadic individuals, we would expect higher NSD values in summer than in winter and for migratory individuals, higher values in winter. We again normalized the difference in NSD values to re-scale the variable to between 0 - 1. We used the following equation:

$$P = 1 - (p2 - p1)$$

Finally, we calculated MPM as an average between the first criterion (R) and the combined second and third criteria ($D \times P$). We combined the second and third criteria because they were statistically more similar compared to the first criterion, looking at the correlation plots and data distribution. MPM thus measures a tendency for migration where individuals close to 0 are more nomadic and individual close to 1 are more migratory. The final equation was calculated as:

$$MPM = \frac{R + (D \times P)}{2}$$

Representative MPM values with corresponding NSD profiles and trajectories are presented in Figure S2.1. Movement patterns of all trajectories determined using MPM are illustrated in Figure 2.2. We validated our method by comparing MPM values with a visual inspection of NSD profiles. Details of the validation and comparison between MPM and the method by Bunnefeld et al. (2011) are provided in the Suppl. material "Method comparison". The R code for calculating MPM is provided in the Suppl. material "R code for Movement Pattern Metric (MPM)".

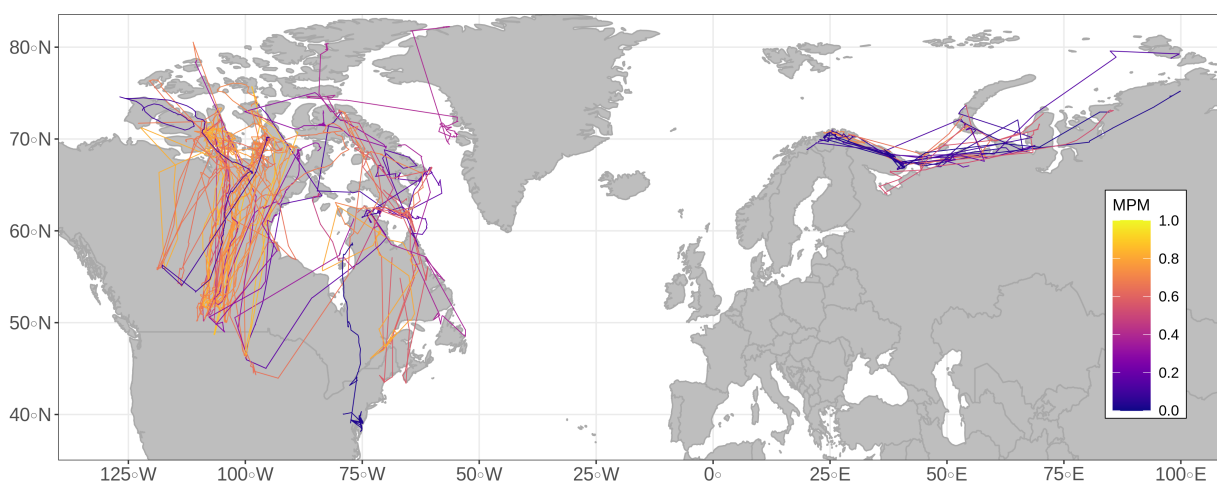


Figure 2.2. Argos and GPS positions of 55 snowy owl annual trajectories. Dark colour (0) represents a tendency for nomadism and light colour (1) tendency for migration.

Utilization distribution

To identify the areas individuals occupied during their annual cycle, we quantified Utilization Distributions (UD) for each trajectory using the R package "move" (Kranstauber et al. 2013). First, we calculated the dynamic Brownian motion variance with a window size of 17 locations, a margin of 3 and a location error of 100m for GPS and 1000m for Argos data (which match the highest location error in our data). From the dynamic Brownian motion variance we then computed dynamic Brownian Bridges on a spatial raster with a 1000m grid cell size and with value 2 for the extension of the bounding box around the animals' tracks. The values for margin and window size were selected based on the guidelines provided by Kranstauber et al. (2012) and the limitation of the sample size of trajectories. From the resulting raster, we selected 99% of the volume of the raster area to exclude areas with

very low probabilities (close to 0). UD values thus represent the proportional probabilities of an individual occupying or using a specific area (raster cell) during its movements.

Resource variability and use

We assessed resource variability and use by comparing NDVI (Normalized difference vegetation index) with the probability values of the UD rasters. NDVI has been used as a proxy for primary productivity (Pettorelli et al. 2011) and as a proxy for vole and lemming activity (Olofsson et al. 2012) (the main food source of snowy owls during the breeding season) and is correlated with several environmental variables i.e. temperature and snow cover (for an example see Curk et al. (2020)). Thus, NDVI can serve as a proxy for resources and/or environmental conditions which the snowy owls were experiencing.

We annotated UD rasters with NDVI modis product MOD13A3 v6 with a resolution of 1 km and 1 month through the open-source Env-DATA system (Dodge et al. 2013). To quantify resource variability, we annotated each UD raster cell on every first day of the month from January 1st, 2001 to January 1st, 2020, resulting in 229 dates. For each raster cell, we quantified intra- and inter-annual variability. Intra-annual variability was calculated using the standard deviation (SD) of NDVI within each year and then average across all years, and inter-annual variability was calculated using the mean of NDVI within each year and its SD across all years. We summed the values of intra- and inter-annual variability in a combined variable of variability (as in Loe et al. (2005)). Then we calculated maximum variability for each raster to have one value for each individual trajectory. We also quantified the proportion of time spent in each cell by dividing the UD value of each cell with the sum of all UD values of the raster. For each raster cell, we then multiplied the proportion of time spent in a cell with the variability value in NDVI for that cell and finally, we calculated the sum of these values for each raster to get one value representative of the resource variability associated with the area used for each individual trajectory.

To estimate resource use, we also annotated UD raster cells for the year matching the time span of the specific individual trajectory (first day of the month from July 1st to June 1st of the following year), resulting in 12 dates. We first calculated the average NDVI of the 12 months to get one value for each raster cell of the UD raster. Finally, we repeated the steps above to estimate the proportion of time spent in each cell, multiplying it with the NDVI value for each cell and summing these values for each raster to get one value

of resource use for each individual trajectory. Resource use can represent a potential for energy intake by the snowy owls since if an individual stay within a specific area, we can expect it is for the purpose of feeding.

Statistical analyses

We used a linear mixed model (LMM) from the "lmerTest" R package (Kuznetsova et al. 2017) and the restricted maximum likelihood method to compare the overall environmental variability (square root transformed) experienced among individuals with different movement patterns. We included Movement Pattern Metric (MPM) as a response variable, the use of maximum resource variability as a predictor, and individual ID as a random effect.

To test whether individuals spent more time in areas with low resource variability, we used linear mixed effects models (LME) from the "nlme" R package (Pinheiro et al. 2021). We ran ten models with the square root of variability as a response variable, the proportion of time spent in each cell (corrected UD re-scaled to 0-1) as a predictor, and individual trajectory nested in individual ID as a random effect. Because of the limitation of the computing power, we included in each model a random sample of 0.05% (5.655 out of 11.310.897) data points. In addition, since the sub-sample of data was still spatial auto-correlated (Moran's I auto-correlation index was < 0.001 ; "ape" R package (Paradis & Schliep 2019)) we included in the LMEs correlation structure with longitude and latitude of each UD raster cell. Finally, we averaged the models using R package "MuMIn" (Barton 2019).

We further used LMMs to investigate whether the use of areas with different resource variability and the resource use i.e. potential for energy intake is comparable between individuals with different movement patterns. First, we included Movement Pattern Metric (MPM) as a response variable, the use of resource variability as a predictor, and individual ID as a random effect. Second, we used MPM as a response variable, resource use as a predictor variable and individual ID as a random effect.

CIs (95%) of the predictors were computed by a bootstrapping method and 500 simulations using generic R function "confint". As an overall test for the significance of predictors, we used full-null model comparison where we compared the full model with the model excluding a fixed effect (Forstmeier & Schielzeth 2011). Validations of our models confirmed the normal distribution of the model residuals, the equal variances when comparing residuals vs fitted values and no indication for heteroscedasticity when

comparing residuals with predictor variables.

Results

Snowy owls exhibited a broad range of movement patterns, from an MPM value of 0.02 (a tendency for nomadism) to 0.87 (a high tendency for regular migration). For 15 out of 39 individuals, we had more than one year of data and changes in MPM for ≥ 0.50 occurred in four out of 16 cases. From those, in three cases changes occurred towards regular migration and in one case towards nomadism. There was a pattern of decrease in MPM from Western North America towards Eurasia (Figure 2.1). In western North America, the majority of tracks represented a tendency for migration while in Eurasia there was a higher tendency for nomadism, and in eastern North America, a combination of tendencies in both directions was observed.

Individuals with a tendency for nomadism generally experienced higher resource variability than those with a tendency for regular migration (full-null model comparison: $\chi^2 = 5.85$, $df = 1$, $P = 0.016$; Table 2.1; Figure 2.3A). The snowy owls, irrespective of their movement patterns, allocated however similar proportions of time to areas with low and high resource variability (Table 2.2; Figure 2.3B; Note that full-null model comparison was not possible for an averaged model). The use of areas with different levels of resource variability was comparable between individuals exhibiting contrasting movement patterns (full-null model comparison: $\chi^2 = 0.10$, $df = 1$, $P = 0.750$; Table 2.3; Figure 2.3C). Finally, the potential for resource use or energy intake did not differ between individuals with different movement patterns (full-null model comparison: $\chi^2 = 0.16$, $df = 1$, $P = 0.692$; Table 2.4; Figure 2.3D).

Discussion

Snowy owl populations and individuals exhibited a range of contrasting movement patterns, from a tendency for nomadism to a tendency for migration. From individuals that we had more than one year of available data, changes of at least 50% occurred in 25% of the cases, which implies that snowy owls are flexible in their movement and can rapidly change movement patterns from one year to another. Such flexibility in movement patterns

Table 2.1. Linear mixed model with the Movement Pattern Metric (MPM) as a response variable, maximum resource variability as a predictor variable, and bird ID as a random effect. CIs (95%) of the predictor were computed by bootstrapping method and 500 simulations using generic R function "confint".

Term	Estimate	Std. Error	lower CI	upper CI	t value	p value
Intercept	0.8	0.1	0.5	1.0	6.1	
Max. res. variab.	-0.6	0.2	-1.0	-0.1	-2.5	0.015*
Random effects	Variance			Std. Dev.		
Bird ID	0.0			0.1		
Residual	0.1			0.3		
Observations	55					
$N_{individual}$	39					
Marginal R^2	0.11					
Conditional R^2	0.15					

Table 2.2. Model averaging of ten LMEs with the square root of variability as a response variable, the proportion of time spent in each cell (corrected UD re-scaled to 0-1) as a predictor, individual trajectory as a random effect and correlation structure with longitude and latitude of each UD raster cell. CIs (95%) of the predictor were computed by bootstrapping method and 500 simulations using generic R function "confint".

Term	Estimate	Std. Error	lower CI	upper CI	z value	p value
Intercept	0.5	0.0	0.7	0.5	43.3	
UD	-3.7	4.6	-12.8	5.3	0.8	0.415
Observations	5655					
$N_{individual}$	55					
$N_{trajectory}$	39					

has been found in other animals such as giant tortoises (Bastille-Rousseau et al. 2016, 2017) and moose (Bunnefeld et al. 2011, Singh et al. 2012). In 75% of cases, changes occurred towards migration which is unexpected considering the expectation that high environmental predictability drives migration and ongoing environmental change is likely to cause increasing environmental predictability (Post et al. 2009, Verboom et al. 2010). However, this shifting occurring on a small scale (from one year to another) is likely caused by year-to-year fluctuations in environmental predictability rather than a suspected global pattern of increasing predictability. In all three geographic populations, individuals showed

Table 2.3. Linear mixed model with the Movement Pattern Metric (MPM) as a response variable, use of resource variability as a predictor variable, and bird ID as a random effect. CIs (95%) of the predictor were computed by bootstrapping method and 500 simulations using generic R function "confint".

Term	Estimate	Std. Error	lower CI	upper CI	t value	p value
Intercept	0.5	0.1	0.3	0.7	4.5	
Use of res. var.	-0.2	0.5	-1.3	0.9	-0.3	0.746
Random effects	Variance			Std. Dev.		
Bird ID	0.0			0.1		
Residual	0.1			0.2		
Observations	55					
$N_{individual}$	39					
Marginal R^2	0.00					
Conditional R^2	0.22					

Table 2.4. Linear mixed model with the Movement Pattern Metric (MPM) as a response variable, resource use as a predictor variable, and bird ID as a random effect. CIs (95%) of the predictor were computed by bootstrapping method and 500 simulations using generic R function "confint".

Term	Estimate	Std. Error	lower CI	upper CI	t value	p value
Intercept	0.5	0.0	0.4	0.6	10.3	
Resource use	-0.0	0.0	-0.0	0.0	-0.4	0.699
Random effects	Variance			Std. Dev.		
Bird ID	0.0			0.1		
Residual	0.6			0.3		
Observations	55					
$N_{individual}$	39					
Marginal R^2	0.00					
Conditional R^2	0.17					

a mix of movement patterns. However, there was a trend towards a W-E gradient in movement patterns with the majority of the western North American population showing rather a migratory behaviour and the majority of the Eurasian population showing a tendency for nomadism, with the western North American population showing mixed patterns.

As hypothesized, our results showed that resource variability drove movement patterns in snowy owls where individuals with a tendency for migration experienced overall lower

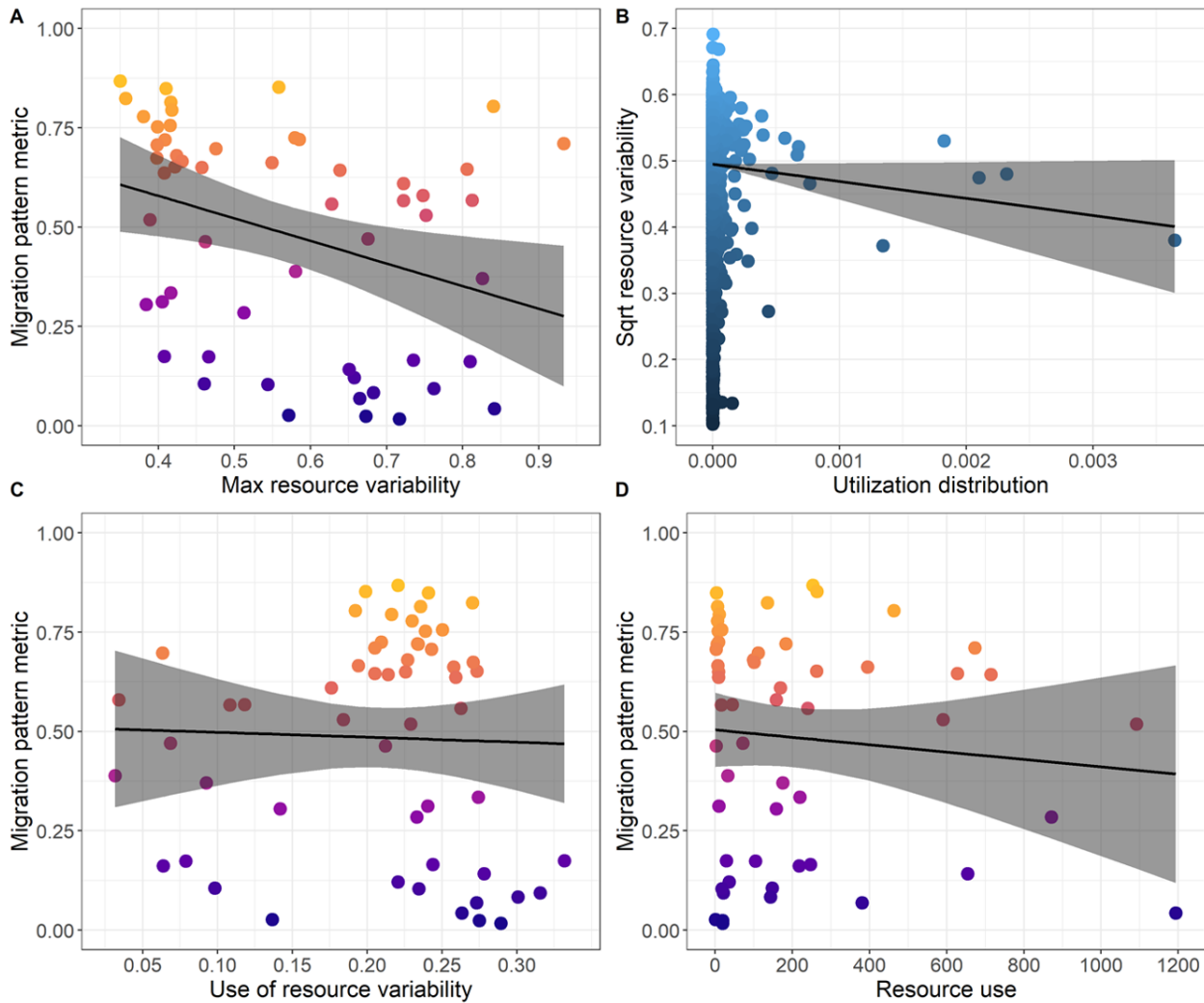


Figure 2.3. The relationship between (A) the movement patterns (MPM - Movement Pattern Metric) and maximum resource variability experienced, (B) sqrt of the resource variability and utilization distribution, (C) the movement patterns and use of resource variability and (D) the movement patterns and resource use i.e. potential for energy intake. Colors from darker to lighter represent (A, C, D) MPM values from 0 - tendency for nomadism to 1 - tendency for migration and (B) resource variability from low to high.

resource variability during their annual movements than individuals with a tendency for nomadism. A previous study showed similar results in the very contrasting study system (Bastille-Rousseau et al. 2017) of the Galapagos Giant Tortoises' altitudinal migration. However, our study expands upon previous work by assessing movement patterns at the continuous, rather than discrete scale, which provides a more precise and innate determination of the emergence of movement patterns in response to environmental variability. Against our expectations in our second hypothesis, the individuals with a tendency for nomadism and overall higher experienced environmental variability did not

spend a higher proportion of their time in areas with higher resource variability. This suggests that all individuals, irrespective of the movement patterns exhibited, allocated similar amounts of their time to areas with different resource variability. They thus seem to have adjusted their movements according to the current levels of resources encountered. Especially nomadic individuals that experienced high fluctuations in resources would thus have been forced to move around more in order to find areas with higher resource levels in which they would spend similar amounts of time as their more migratory counterparts. Consequently, individuals exhibiting regular movement have experienced more stable and predictable levels of resources and might therefore moved in a more consistent way. In accordance with our third and fourth hypothesis, individuals with different movement patterns spent a similar proportion of time in areas with comparable levels of resource variability and had a similar potential for resource use i.e. energy intake. All results considered, the contrasting movement patterns are the response of snowy owls to different resource variability in the environment they encountered securing access to comparable levels of energy.

The individuals with contrasting movement patterns should according to our findings collect the same energy overall, but nomadic individuals have to move more to achieve the same outcome. This suggests that regular migrants are more efficient in accumulating energy than nomads. We would therefore expect that there is a trade-off between the amount of movement that is needed to achieve the apparently required level of using space providing the necessary resources.

Ongoing global environmental change is influencing environmental variables such as temperature, snow cover, NDVI and rain-on-snow events (Post et al. 2009, Bhatt et al. 2010, Serreze & Barry 2011). Even the predictability of prey distribution and availability for many predators including snowy owls is changing (Ims et al. 2008) (but see Ehrich et al. (2020)). There is growing evidence that environmental conditions will become less predictable (Post et al. 2009, Verboom et al. 2010) which might cause snowy owls to become eventually strictly nomadic. With more individuals becoming nomadic, also population densities might become lower, because collecting the same amount of energy will require more investment in movement and therefore the overall allocation of energy into offspring might be reduced. Also, the changing patterns in movement might affect the genetic structure of the populations and could affect important aspects such as local adaptation, population divergence and

ultimately speciation.

In addition, less flexible and strictly migratory species might not be able to adapt rapidly enough to the environmental change. While more flexible and strictly nomadic species might have higher phenotypic plasticity in comparison to migrants, and thus more easily adapt to the new environmental conditions. Thus, from a conservation perspective, we would need to focus our efforts on less flexible regular migrants. On the other hand, nomadic individuals with their unpredictable movements represent a greater conservation challenge than migratory individuals for which protected areas can be easily determined (Teitelbaum & Mueller 2019).

Conclusions

Our study demonstrates that the contrasting movement patterns found between individuals are caused by their response to the different resource variability in the environment in order to secure comparable levels of access to resources i.e. potential for energy intake. These findings have important implications for the conservation of the species especially because global environmental conditions are expected to become less predictable (Post et al. 2009, Verboom et al. 2010). We expect that nomadic species with higher movement flexibility in comparison to regular migrants might be able to more easily adapt to the new environmental conditions. At the same time, the animal movement might shape environmental predictability by for example habitat use and predation (Riotte-Lambert & Matthiopoulos 2020). So further research is needed to understand the feedbacks between animal movement and environmental predictability (Riotte-Lambert & Matthiopoulos 2020). Furthermore, the findings of this study provide an opportunity for future research to investigate the potential to use changes in movement patterns as an indicator for environmental change.

Acknowledgements

We thank Norwegian Nature Inspectorate (SNO) in Finnmark, Fjelltjenesten, Statskog (The State-owned Land and Forest Company) in Troms and Nordland for assistance in the field with catching snowy owls in Norway. For helping to trap owls in Canada we thank Dan Zazelenchuk, Marten Stoffel, Mike Blom, Erhard Pletz, Mike Russel and for the help in the

eastern part of Canadian Arctic, we thank Audrey Robillard. For assistance in trapping owls in the US, we thank Mike Lanzone, Nova Mackentley, Tom McDonald, Chris Neri, Norman Smith, and Matt Solensky.

Chapter 3

Arctic migratory raptor selects nesting area during the previous breeding season

Teja Curk, Olga Kulikova, Ivan Fufachev, Martin Wikelski, Kamran Safi,
Ivan Pokrovsky

In preparation

Abstract

1. Migratory birds that breed in the Arctic are challenged with short summers limiting the time for selecting a suitable nesting area. Rough-legged buzzards (*Buteo lagopus*), as many other arctic predators, rely on rodent cycles during the breeding season, a 3-5 year period where lemming and vole abundance rises for a few years, reaching a peak to crash afterwards. However, it remains unclear how arctic predators, especially migrants, can find the area with peaks in rodent abundance during the very short selection period available.
2. We hypothesized that successful breeders return in the following year to the same nesting area, while failed breeders search for an alternative nesting area during the same breeding season and the following year return to that area. We predicted that (i) successful as well as failed breeders would stay in the Arctic during the post-breeding period, (ii) prospecting movement, i.e. potential search for a nesting area, would be more evident in failed than in successful breeders, (iii) in the following year, successful breeders will return to the same area and failed breeders will return to the alternative area they found during the previous breeding season.
3. Between 2013 and 2020, we tracked 43 adult rough-legged buzzards. In addition to the GPS positions, we also collected information on the nest locations of the breeding individuals and nesting success. In cases when field observations were absent, we estimated nest locations and inferred nesting success using GPS and accelerometry data.
4. The results showed that rough-legged buzzards, regardless of the breeding success, stayed in the Arctic until the end of the summer. Failed breeders prospected more by travelling larger distances, covering larger areas and moving farther away from the nest than successful breeders. However, successful breeders did not return to the same area to breed and in some cases failed breeders did return to the same area. Yet, both failed and successful breeders nested in the area they inspected in the previous season.
5. Our study suggests that the arctic migratory rough-legged buzzards search for nesting area already during the previous breeding season. Such time management, which is to our knowledge described for the first time, may be used by other migratory Arctic breeders. This study thus provides a step forward towards understanding movement and settlement decisions in animals experiencing highly seasonal and changing environmental conditions.

Introduction

The decision of animals to inhabit a specific area is of significant importance for their reproduction success and survival (Montgomery & Roloff 2013). Particularly so in migratory species that travel large distances and thus have very little time after their arrival to the breeding grounds to choose an appropriate location for reproduction. This lack of time is especially evident in arctic migrants which are particularly limited by a short breeding season (Bêty et al. 2004, Madsen et al. 2007, Lamarre et al. 2017). Another limitation for migratory arctic species is the timing of migration. Spring migration and the options for arrival to the breeding area are limited in time by the photoperiod and extreme environmental conditions on the breeding grounds such as low temperature, scarcity of food and snow cover (Curk et al. 2020). Another aspect to consider is the fluctuating environment of the Arctic during the reproductive season. Environmental conditions, including food resources, fluctuate highly and arctic predators, which rely on lemmings and voles as their main food source, must efficiently track or predict this variable resource.

A key component of life in the tundra habitat is the rodent cycle (with the differences in amplitude of more than 100 fold) representing an abundant resource for numerous predators such as the stoat (*Mustela erminea*), arctic fox (*Vulpes lagopus*), long-tailed skua (*Stercorarius longicaudus*), snowy owl (*Bubo scandiacus*) and rough-legged buzzard (*Buteo lagopus*) every three to five years (Gilg et al. 2003, Sundell et al. 2004, Gilg et al. 2006, Tast et al. 2010). The cycle is defined by a period where lemming and vole abundance rises for a few years, reaches a peak and afterwards crashes (Oksanen & Oksanen 1992, Angerbjörn et al. 2001). The rodent cycle, which appears as a pulsed resource, can be at the peak in one area while it might be at its lower point in another within the same season (Predavec et al. 2001, Krebs et al. 2002). While resident predator species staying year round in the Arctic can track this pulsed and spatially heterogeneous resource (Tarroux et al. 2010, Therrien et al. 2014), it remains unclear how migratory species that spend only a limited time in the Arctic find the areas with rodents' peak during the concise settlement decision process.

To tackle this question, we used as a model species a migratory arctic breeder, the rough-legged buzzard. This species specialises in small rodents during the breeding season. However, it can breed in areas with no rodents and shift to alternative prey (Ferguson-Lees & Christie 2001, Bechard & Swem 2002, Pokrovsky et al. 2014, 2015). Yet, small rodents

are the preferred food source for buzzards and feeding on rodents (at its peak) during the breeding season results in higher breeding success of individuals (Sundell et al. 2004, Tast et al. 2010). Rough-legged buzzards in our study breed either in the areas with a cyclic density of rodents (Nenetsky, Vaigach and Yamal) or in areas with no rodents (Kolguev Island), where a variety of geese species breed in large numbers annually (Mooij et al. 2011), providing a stable resource for the rough-legged buzzard (Pokrovsky et al. 2015). Thus, areas with rodent cycles are for the purpose of this study classified as "variable resource" areas and areas with no rodents, as "stable resources".

The typical shape of the cycle consists of four years with about three years of increasing rodent numbers (from low to medium to peak abundance) followed by a rapid crash thereafter (from the peak to low abundance) (Oksanen & Oksanen 1992, Angerbjörn et al. 2001). Thus, if arctic predators were to predict rodent abundance for their next breeding season, they would win in three, and lose in one, out of four cases. Therefore, if rodent abundance is high enough for successful breeding, individuals should return to the same nesting area in the following year. Successful breeders would thus stay in their nesting area until the end of the breeding season, afterwards migrate South to overwinter and return in spring to the same area for breeding. If, however, rodent abundance was low, buzzards would fail to breed. An individual who failed to breed would thus leave the nesting area in search for a suitable future nesting area for the following year. After such a phase of prospecting movement, i.e. potential search for a nesting area, it would migrate to the wintering area, and after returning from spring migration, attempt to breed in a suitable nesting area that it had found in the previous summer. The hypothesis is illustrated on Figure 3.1.

Our specific predictions are as follows: (i) Individuals that failed to breed (either in areas with stable or variable resources) will remain in the Arctic for the rest of the summer and not migrate to the wintering grounds earlier. The departure date from the breeding grounds will thus not differ between successful and failed breeders. We also expect no difference between successful and unsuccessful breeders but also for the non-breeding individuals in the timing of departure. (ii) Individuals who failed to breed will have extra time available during the breeding season to search for a suitable breeding area for the following year. Thus, failed breeders will prospect more (travel larger distances, cover larger areas and move further away from the nest) than the successful breeders. In areas with stable

resources (Kolguyev Island), the reason for breeding failure is usually not a low availability of food resources but nest destruction caused by heavy rain and landslides (Beardsell et al. 2017). Therefore, here failed breeders will also prospect more than successful breeders to find a new breeding area after a failed attempt. However, the scale will be smaller than in areas on the Mainland (variable resources) since food resources are stable and individuals do not need to travel far to find alternative suitable nesting area. (iii) Failed breeders, regardless of areas with stable or variable resources, would return to the exploration area i.e. potential nesting area they selected during the previous post-breeding period. While successful breeders would return to the same area to breed.

Note that throughout the text we use the term "nesting area" for the area where rough-legged buzzards breed, "post-breeding period" for the period in the breeding season after a breeding attempt, "prospecting" for the potential search for a new nesting area during the post-breeding period, and "exploration area" for the area individuals prospected during the previous season and potentially return to in the following breeding season.

Materials and methods

Study area

Fieldwork was conducted in June-August 2013-2019 in NW Russia on four study sites (Figure 3.2): Kolguev Island in the Barents Sea (hereafter Kolguev, $69^{\circ}16'N$, $48^{\circ}87'E$) in years 2013, 2015, 2017-2019; Nenetsky Nature Reserve in the Pechora river lowlands (hereafter Nenetsky, $68^{\circ}20'N$, $53^{\circ}18'E$) in 2014; Vaigach Island (hereafter Vaigach $69^{\circ}43'N$, $60^{\circ}08'E$) in 2015; and "Erkuta" tundra monitoring site in the southern part of Yamal peninsula (hereafter Yamal, $68^{\circ}12'N$, $68^{\circ}59'E$) in 2016. For the details on permits, see the ethical statement in the Suppl. material.

Data collection

Between 2013 and 2020, we tracked 43 adult rough-legged buzzards (35 females and 8 males). We caught birds with bow nets on the nest and equipped them with 45g solar GSM-GPS-ACC loggers (e-obs GmbH) and 15g solar GSM-GPS loggers (UKn - University of Konstanz, Model "Lika") using a Teflon harness. E-obs loggers were attached on 28

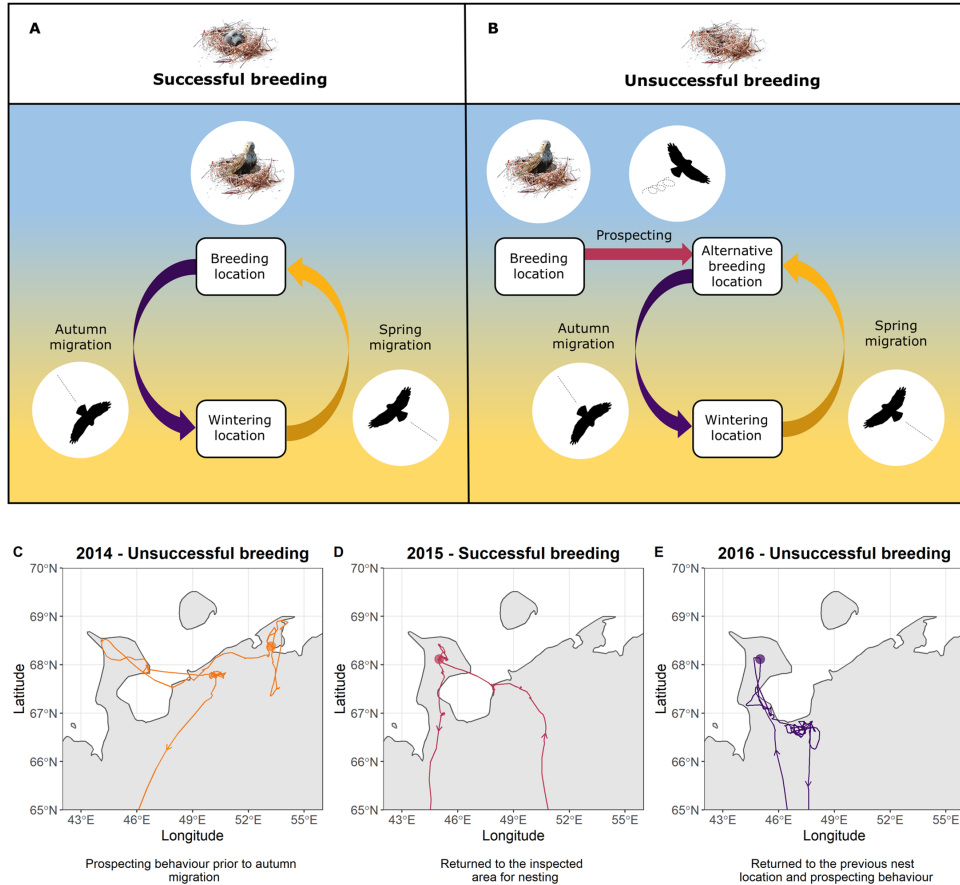


Figure 3.1. The overall scheme of the hypothesis. (A) If an individual breeds successfully, it stays within the nesting area until the end of the breeding season, afterwards migrates to the south to overwinter and in spring returns to the same area for breeding. (B) If an individual fails to breed, it leaves the nesting area and searches for a suitable nesting area for the following year. After this phase of prospecting movement, it migrates to the wintering area and after spring migration, it attempts to breed in the suitable nesting area that it found in the previous summer. (C, D, E) Exemplary trajectories of one individual for three consecutive years. Nest locations are marked with dots and arrows represent movement direction.

individuals, UKn loggers on 13 and two individuals were first equipped with UKn loggers that were later replaced with e-obs loggers. E-obs loggers recorded GPS locations and 3D body acceleration during 24 hours/day. GPS positions were recorded every hour (full battery) and every 5 hours (normal battery). Three-axial body acceleration was measured every 5 min for 3.8 s at 10.54 Hz (40 data points per axis and 120 data points per ACC burst). Data were stored and then downloaded via GSM mobile phone network using GPRS technology or via UHF radio link using handheld base stations. UKn loggers recorded GPS positions every hour (full battery) and every 12 hours (normal battery) 24 hours/day.

In addition to the GPS data, we also collected information on the nest locations of the breeding individuals and the nesting success for each year ($n = 87$). We recorded nest location and nesting success for 40 annual trajectories of individuals (9 for males and 31 for females) using direct field observations. For 47 annual trajectories (all of them females), we estimated the location of the nest and inferred nesting success from the bio-logging data (GPS and accelerometer) in the following way: If the bird stayed in one place (the difference between coordinates was $< 3\text{m}$) for more than one day (24 hourly positions), we considered it as the beginning of incubation and this position as the nest coordinates. We verified this assumption with information about the bird's body's position for birds for which we used loggers with accelerometers (28 bird-years). In all cases, the accelerometer showed that the birds at this time were in a horizontal position, which is possible if the bird is flying, or incubating a clutch or covering the nestlings. If the bird stayed on the nest for more than 50 days from the start of incubation, we considered it a successful nest. The threshold of 50 days was used because the incubation period in wild rough-legged buzzards is at least 31 days (Cramp & Simmons 1980) and after hatching, a female stays at the nest more or less continuously until young are 17-22 days old (Bechard & Swem 2002). If a bird stayed less than 50 days in a nest, we assumed that it failed to breed. We verified our distinction between the failed and successful breeders with the direct observations, and in all cases, we correctly predicted nesting and breeding status. Therefore, for 87 annual trajectories, we estimated breeding attempt and if a bird tried to breed, we estimated the nest coordinates. For 70 annual trajectories, we estimated the nesting success (successful/failed) and nesting duration (number of days the bird was incubating and feeding nestlings).

Data analyses

After removing outliers and duplicated timestamps, the data set comprised 43 individuals, 133 annual trajectories and 268.977 positions (Figure 3.2).

First, we investigated the relationship between the departure day from the breeding grounds and nesting performance. For each individual trajectory (GPS locations of a bird during the specific year), we noted the date when it crossed the latitude of 64 degrees (the approximate southern border of the breeding area of the rough-legged buzzard in this region) during the autumn migration. If the difference in days, between the first GPS position before and the first position after a bird crossed the 64 degrees latitude, was less

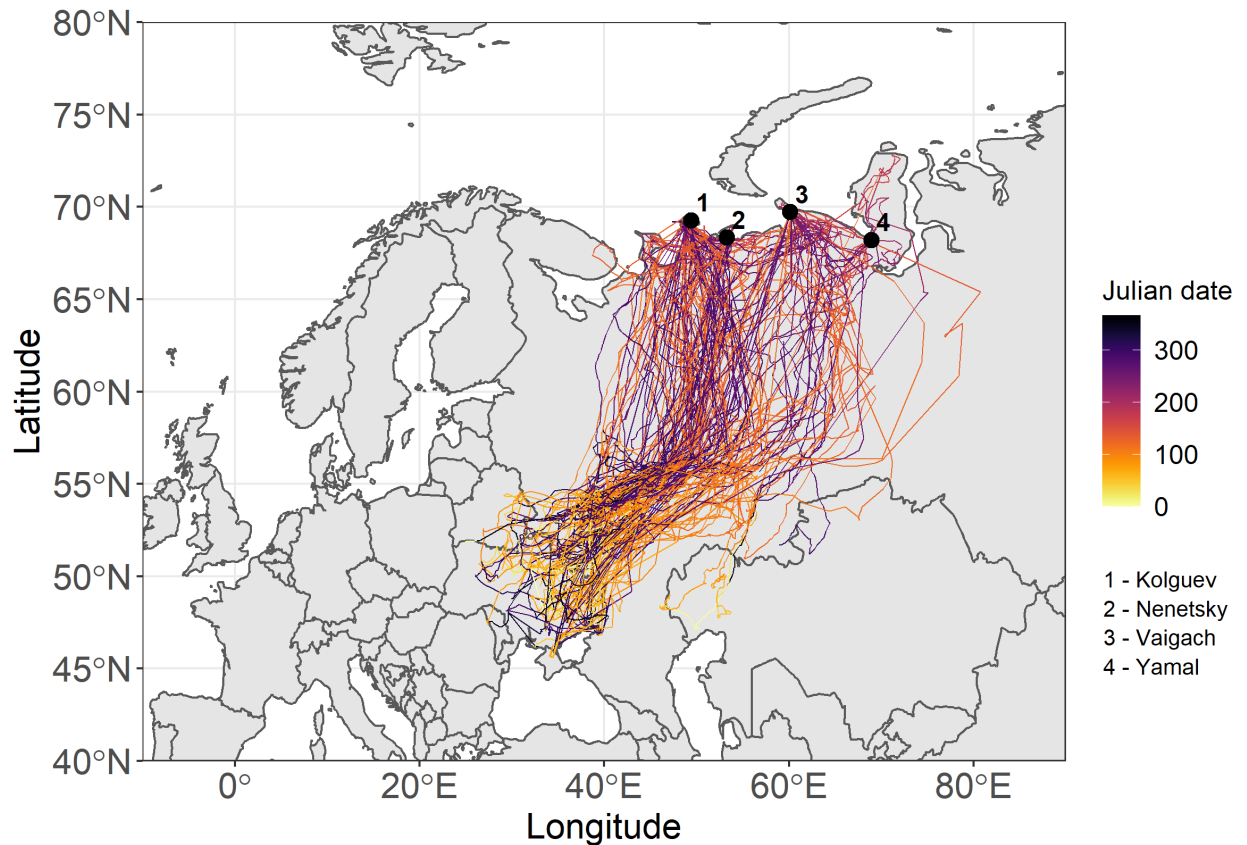


Figure 3.2. GPS trajectories of 43 rough-legged buzzards (133 annual tracks). The colour gradient represents Julian date. Locations of the study sites are marked with black dots.

than 10 days we used the mean value as a departure location and its corresponding date as departure day. If the difference was more than or equal to 10 days, we did not use the departure day for the analysis as the calculated mean location was not likely to represent the departure location and thus, departure day reliably. In total, we had 71 departure days for 35 birds from 2013-2020. When individuals crossed latitude of 64 degrees more than once, we recorded the first crossing as a departure/arrival location.

Second, we compared prospecting movement after breeding attempt between the individuals who failed to breed and those who bred successfully (Figure 3.1). In addition, we compared prospecting movement between the individuals that bred in an area with stable resources and those that bred in an area with variable resources. Prospecting movement was assessed for GPS locations between the nest location and the location corresponding to the date of 10 days before the departure location. The threshold of 10 days was selected based on visual inspection of a different set of locations included with different thresholds.

By removing 10 days before departure, we made sure to include only locations that are a part of prospecting movement and avoided including locations that were already part of autumn migration. Prospecting movement was quantified by the cumulative distance (using "move" R package Kranstauber et al. (2019)), area covered using the 95% MCP - Minimum Convex Polygon estimator ("adehabitatHR" R package Calenge (2006a)), and the distance from the nest to each GPS location (using "raster" R package Hijmans (2019b)). The three parameters were calculated by including the first five data points (GPS locations) and every step adding an additional data point (e.g. 95% MCP was estimated for the first five locations, then again for six locations, for seven locations, etc. until all locations were included). In total, we calculated the three parameters for 14 individuals that bred in an area with stable resources (5006 data points) and 13 individuals that bred in an area with variable resources (4686 data points).

Third, we assessed whether individuals that failed to breed the following breeding season returned to the same area they inspected the year before i.e. exploration area and attempted to breed (Figure 3.1B). To test whether individuals inspected the area they returned to the following year to breed, we calculated the minimum distance between each GPS location of an individual's annual trajectory to the nest location of the following year (using "sp" R package Pebesma & Bivand (2005), Bivand et al. (2013)). We calculated these trajectory-to-nest distances for individuals that failed to breed and those that bred successfully for a total of 18 individuals (35 data points). To test if successful breeders return to the same area to breed and failed breeders to the different area, we calculated the distance between the nest locations of the the current and the following year (20 individuals, 37 data points) and compared them between the failed and successful breeders.

Statistical analysis

We tested whether rough-legged buzzards stay in the Arctic until the end of the breeding season, regardless of the nesting success and duration. We ran a linear mixed model (LMM) with departure day as a response variable, nesting success as a fixed effect and bird ID as a random effect, and a linear model (LM) with departure day as a response variable and nesting duration as a predictor. To account for pseudoreplication in the LM, we ran ten models each with one year per individual included (years per individual included in each model were randomly selected) and performed model averaging. We additionally checked

whether the sex of individuals or season (year) influence departure days. We used LMMs with departure days as a response variable, year as a fixed effect and bird ID as a random effect. We ran 10 LMs and performed model averaging as described above.

Next, we investigated if failed breeders prospected during the post-breeding period more than the successful breeders and if this difference was more pronounced in individuals breeding in areas with variable than in areas with stable resources. Prospecting behavior of individuals that bred successfully and those that failed to breed was investigated using LMMs with log cumulative distance, log MCP or log trajectory-to-nest distance included as a response variable, an interaction between the Julian day and nesting success as a predictor and annual trajectory identity as a random effect. We ran the three models separately for stable and variable resources and performed a model averaging of 10 models, so that in each model, only one bird ID per annual trajectory was included. The inclusion of annual trajectory in the models was randomly selected. To be able to average the models, the sample sizes of data sets used for models had to be the same, thus we used an approximate minimum sample size of randomly selected rows per annual trajectory included ($n = 1800$ for stable resources and $n = 2000$ for variable resources).

For all models, we first performed an overall test of full-null model comparison. We fitted the LMMs with a restricted maximum likelihood method using lmerTest (Kuznetsova et al. 2017). Model averaging was performed using the "MuMIn" R package (Barton 2019). Assumptions of normally distributed and homogeneous residuals were fulfilled.

Results

Departure days

Rough-legged buzzards stayed in the Arctic during the post-breeding period and the timing of departure from the breeding grounds was similar for the individuals that bred successfully (mean $\pm$ SE: 276.4 ± 1.9 , $n = 29$) and those that failed to breed (mean $\pm$ SE: 278.8 ± 1.6 , $n = 27$). Five individuals which did not attempt to breed departed from the breeding grounds at the similar time than the other two groups (mean $\pm$ SE, 272.0 ± 4.3 , $n = 5$). The model results confirmed that failed and successful breeders departed from the breeding grounds at the approximately same time (full-null model comparison: $\chi^2 = 1.56$, $df = 1$, $P =$

0.21; Table 3.1; Figure 3.3). Also, nesting duration of individuals that failed to breed did not influence the timing of departure (Table 3.2; Figure 3.3). Note that no full-null comparison for this model is provided since we performed model averaging and we used only one annual trajectory per individual (Sum of squares = 3.65, df = 1, P = 0.814).

Departure days significantly differed between the years (2013 - 2020) with the timing of departure becoming later every year (full-null model comparison: $\chi^2 = 34.45$, df = 7, P 0.001; Table S3.1; Figure S3.1). However, each year, we had a similar proportion of successful vs failed breeders (mean $\pm$ SE; failed: 4.6 ± 1.2 , successful: 4.8 ± 1.0), meaning that our results were not year-dependent.

Table 3.1. Linear mixed model with departure day as a response variable, nesting success as a fixed effect and bird ID as a random effect. CIs (95%) of predictors were computed using the bootstrapping method and 500 simulations in R package "lmer".

Term	Estimate	Std. Error	lower CI	upper CI	t value	p value
Intercept	278.6	1.9	274.6	282.2	143.1	
Nesting success	-2.6	2.1	-7.0	1.6	-1.2	0.223
Random effects	Variance			Std. Dev.		
Bird ID	60.2			7.8		
Residual	37.0			6.1		
Observations	56					
$N_{individual}$	30					
Marginal R^2	0.02					
Conditional R^2	0.63					

Table 3.2. The result of the model averaging with included ten LMs using departure day as a response variable and nesting duration as a predictor. Each model contained a random sample of rows so that only one year per bird ID was included. The output of the conditional and full average of the models was identical. CIs (95%) of predictors were computed by the bootstrapping method and 500 simulations using generic R function "confint". "Observations" is the sample size included in one model.

Term	Estimate	Std. Error	lower CI	upper CI	z value	p value
Intercept	282.4	5.5	270.7	294.1	47.5	
Nesting duration	-0.1	0.2	-0.5	0.2	0.6	0.552
Observations	19					

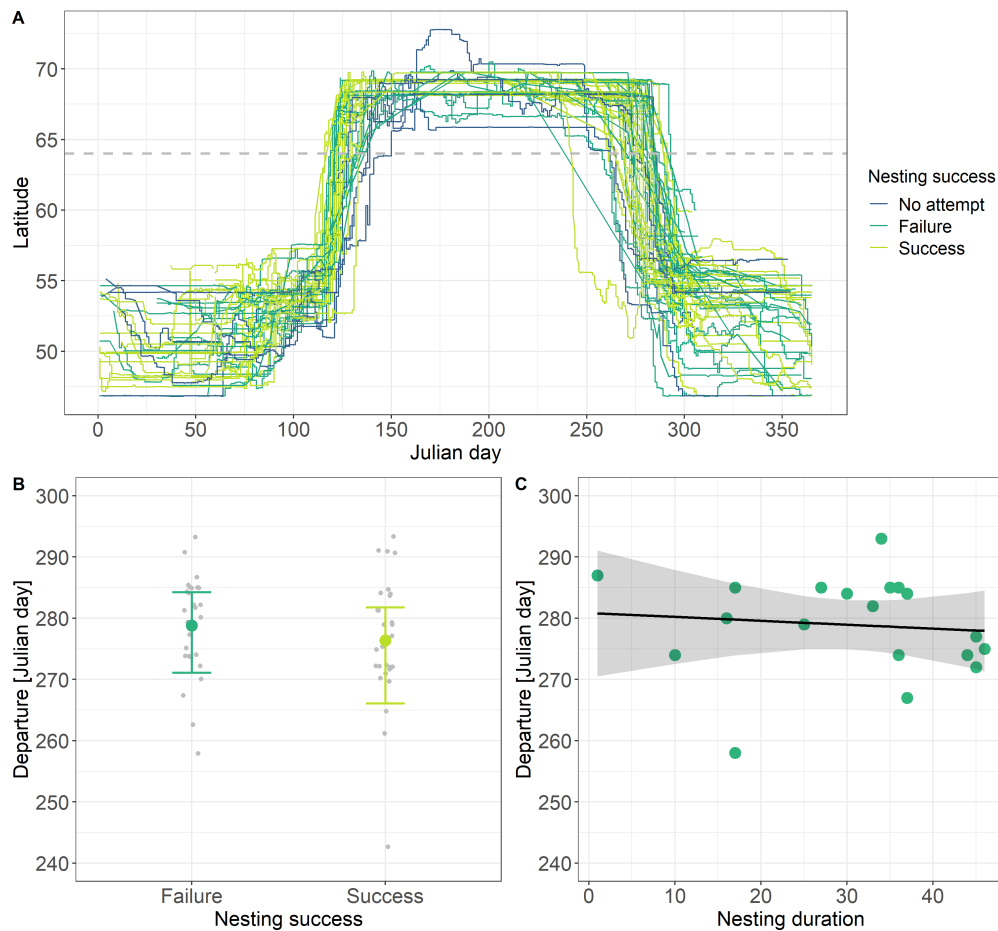


Figure 3.3. Relationship between the nesting success and departure days in rough-legged buzzards. (A) Latitude change during the annual life-cycle. (B) Departure day as a response of nesting success (predicted 95% CIs from LMM using the bootstrapping method and 500 simulations in "ciTools" R package Haman & Avery (2020) with lower limit representing minimum CI and upper limit representing maximum CI; grey dots represent raw data). (C) Departure day as a response of nesting duration of individuals that failed to breed (predicted CIs from LM with only one year of data per individual included; blue dots represent raw data).

Prospecting behaviour

All three parameters measuring prospecting behavior during the post-breeding period, cumulative distance, MCP and trajectory-to-nest distance, had higher values for failed than for successful breeders.

Cumulative distance measured for birds breeding in stable resources increased with Julian day significantly more for individuals that failed to breed than for individuals that bred successfully (full-null model comparison: $\chi^2 = 2287.8$, $df = 3$, $P < 0.001$; Table 3.3; Figure 3.4A). For birds breeding in variable resources, the cumulative distance also increased with Julian day and was influenced by the nesting success (full-null model comparison: $\chi^2 =$

2772.6, df = 3, $P < 0.001$; Table 3.4; Figure 3.4B).

Table 3.3. Linear mixed model with log cumulative distance as a response variable, an interaction between the Julian date and nesting success as a fixed effect and bird ID as a random effect. Only data for stable resources are included. CIs (95%) of predictors were computed using the bootstrapping method and 500 simulations in R package "lmer".

Term	Estimate	Std. Error	lower CI	upper CI	z value	p value
Intercept	-1.0	0.4	-1.7	-0.2	2.5	
Julian date	0.0	0.0	0.0	0.0	42.1	<0.001***
Nesting success	1.0	0.5	0.1	2.0	2.3	0.024*
Jul.date:Nest.suc.	-0.0	0.0	-0.0	-0.0	10.1	<0.001***
Observations	1834					
$N_{individual}$	14					

Table 3.4. Linear mixed model with log cumulative distance as a response variable, an interaction between the Julian date and nesting success as a fixed effect and bird ID as a random effect. Only data for variable resources are included. CIs (95%) of predictors were computed using the bootstrapping method and 500 simulations in R package "lmer".

Term	Estimate	Std. Error	lower CI	upper CI	t value	p value
Intercept	-0.8	0.3	-1.5	-0.2	2.7	
Julian date	0.0	0.0	0.0	0.0	64.5	<0.001***
Nesting success	-3.3	0.5	-4.3	-2.4	7.1	<0.001***
Jul.date:Nest.suc.	0.0	0.0	0.0	0.0	10.1	<0.001***
Observations	2225					
$N_{individual}$	13					

MCP increased with the Julian date and was significantly larger for individuals that failed to breed than for individuals that bred successfully. This effect was seen in individuals that bred in stable resources (full-null model comparison: $\chi^2 = 841.1$, df = 3, $P < 0.001$; Table 3.5; Figure 3.4C) as also for individuals that bred in variable resources (full-null model comparison: $\chi^2 = 1225.9$, df = 3, $P = 0.002$; Table 3.6; Figure 3.4D).

Trajectory-to-nest distance increased with the Julian day and it was significantly larger for failed breeders than for successful breeders. This was the case for individuals breeding in stable resources (full-null model comparison: $\chi^2 = 139.7$, df = 3, $P < 0.001$; Table 3.7; Figure 3.4E) and also for individuals breeding in variable resources (full-null model comparison: $\chi^2 = 1035.8$, df = 3, $P < 0.001$; Table 3.8; Figure 3.4F).

We cannot directly compare the estimates from different models. However, based on

the raw data presented in Figure 3.4, individuals breeding in areas with variable resources explored larger areas and travelled longer distances and further from the nest than those breeding in areas with stable resources.

Table 3.5. Linear mixed model with log MCP as a response variable, an interaction between the Julian date and nesting success as a fixed effect and bird ID as a random effect. Only data for stable resources are included. CIs (95%) of predictors were computed using the bootstrapping method and 500 simulations in R package "lmer".

Term	Estimate	Std. Error	lower CI	upper CI	z value	p value
Intercept	-4.6	0.5	-5.7	-3.6	8.9	
Julian date	0.0	0.0	0.0	0.0	30.7	<0.001***
Nesting success	3.3	0.6	2.2	4.5	5.5	<0.001***
Jul.date:Nest.suc.	-0.0	0.0	-0.0	-0.0	17.2	<0.001***
Observations	1855					
<i>N</i> individual	14					

Table 3.6. Linear mixed model with log MCP as a response variable, an interaction between the Julian date and nesting success as a fixed effect and bird ID as a random effect. Only data for variable resources are included. CIs (95%) of predictors were computed using the bootstrapping method and 500 simulations in R package "lmer".

Term	Estimate	Std. Error	lower CI	upper CI	z value	p value
Intercept	-6.1	1.1	-8.2	-3.9	5.6	
Julian date	0.1	0.0	0.0	0.1	31.3	<0.001***
Nesting success	-2.2	1.4	-4.9	0.5	1.6	0.108
Jul.date:Nest.suc.	-0.0	0.0	-0.0	-0.0	4.3	<0.001***
Observations	2254					
<i>N</i> individual	13					

Return to the explored area

Both groups, successful and failed breeders, returned to the area they explored during the previous breeding season. The minimum distance measured between an individual's annual trajectory and nest location of the following year was very small for the failed breeders (Mean $\pm$ SE: 0.8 ± 0.5 km; $n = 15$) and ten times larger for successful breeders (Mean $\pm$ SE: 10.4 ± 6.8 km; $n = 20$) (Figure 3.5). The reason for a much larger mean value of successful breeders is that there were two outliers present (Figure 3.5B). These are the two

Table 3.7. Linear mixed model with log nest distance as a response variable, an interaction between the Julian date and nesting success as a fixed effect and bird ID as a random effect. Only data for stable resources are included. CIs (95%) of predictors were computed using the bootstrapping method and 500 simulations in R package "lmer".

Term	Estimate	Std. Error	lower CI	upper CI	z value	p value
Intercept	-0.3	0.2	-0.6	0.1	1.6	
Julian date	0.0	0.0	0.0	0.0	12.4	<0.001***
Nesting success	-0.0	0.3	-0.5	0.5	0.1	0.898
Jul.date:Nest.suc.	-0.0	0.0	-0.0	-0.0	7.9	<0.001***
Observations	1835					
<i>N_{individual}</i>	14					

Table 3.8. Linear mixed model with log nest distance as a response variable, an interaction between the Julian date and nesting success as a fixed effect and bird ID as a random effect. Only data for variable resources are included. CIs (95%) of predictors were computed using the bootstrapping method and 500 simulations in R package "lmer".

Term	Estimate	Std. Error	lower CI	upper CI	z value	p value
Intercept	-5.0	0.3	-5.6	-4.3	15.0	
Julian date	0.0	0.0	0.0	0.0	44.3	<0.001***
Nesting success	0.5	0.5	-0.4	1.4	1.0	0.304
Jul.date:Nest.suc.	-0.0	0.0	-0.0	-0.0	14.1	<0.001***
Observations	2271					
<i>N_{individual}</i>	13					

cases where individuals upon spring migration flew in a direction of the nest location of the previous year but decided to settle before reaching that location (Figure S3.2). Thus, after removing these two outliers, the mean ($\pm$ SE) trajectory-to nest distance for successful breeders was $0.6 \pm 0.2\text{km}$ ($n = 18$).

The return to the same nesting area in the following year measured by the distance between the nest locations of the current and the following year was similar between the failed and successful breeders (Figure S3.3). The mean ($\pm$ SE) distance for failed breeders was $29 \pm 17\text{km}$ (range: 2m - 341km) and for successful breeders was $16 \pm 10\text{km}$ (range: 0.3km - 139km). However, the large distance of 341km is from one individual that shifted the nesting after the failed nesting (see its trajectories on Figure 3.1). If we remove this outlier, the mean ($\pm$ SE) distance for failed breeders is $14 \pm 8\text{km}$ (range: 2m - 138km).

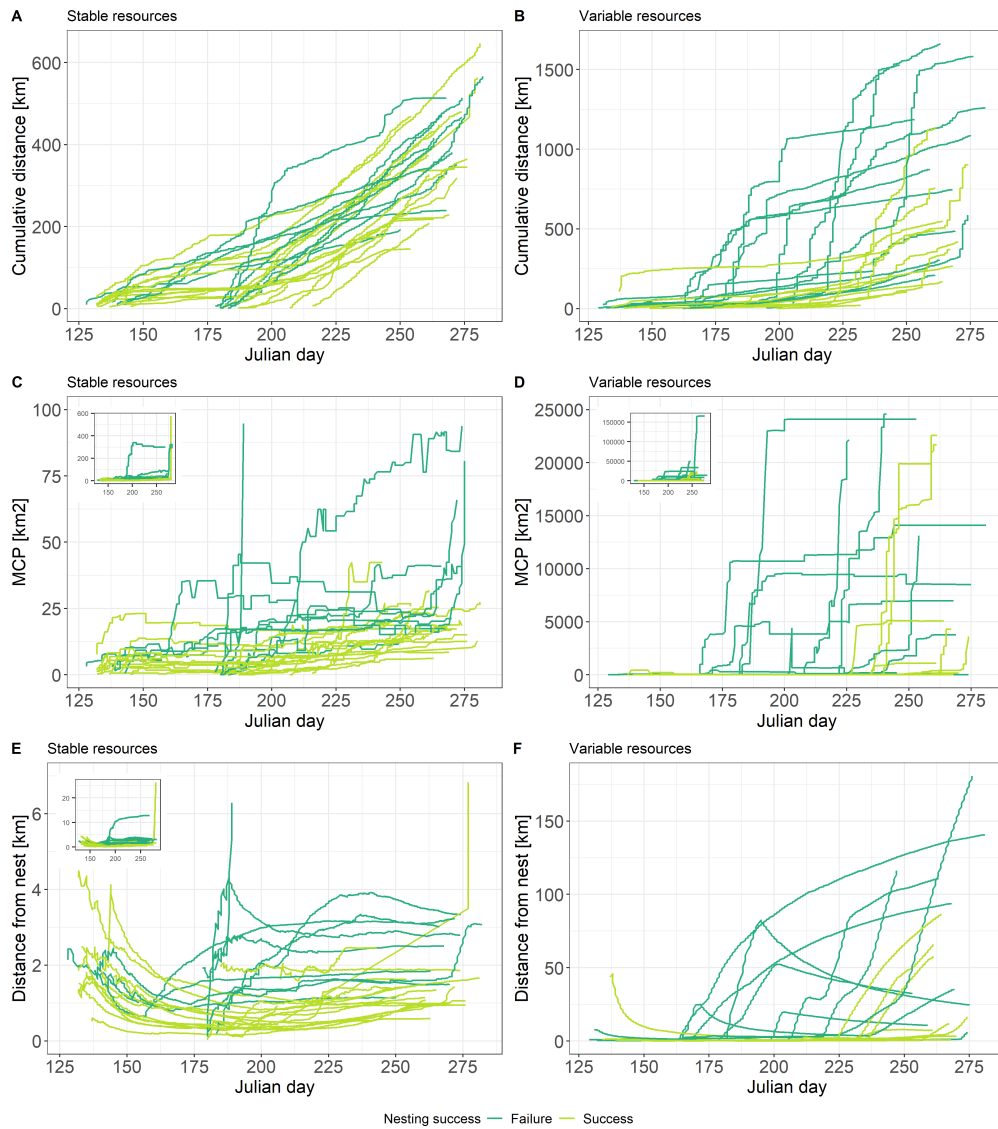


Figure 3.4. (A) Cumulative distance as a function of Julian date for stable resources. (B) Cumulative distance as a function of Julian day for variable resources. (C) MCP as a function of Julian day for stable resources. (D) MCP as a function of Julian day for variable resources. (E) Nest distance as a function of Julian day for stable resources. (F) Nest distance as a function of Julian day for variable resources.

Discussion

We hypothesised that successful breeders return the following year to the same area to breed, while failed breeders search for an alternative nesting area already during the same breeding season and the following year return to that area for breeding.

However, we did not find evidence for this behaviour from our data. There seems to be a high variation among the movements of the rough-legged buzzards and their return to the same or different nesting area the following season. Yet, we clearly showed that

rough-legged buzzards return and attempt to breed in the exploration area i.e. the area they inspected the year before. This result suggests that rough-legged buzzards select nesting area already during the previous breeding season.

First, we showed that the departure date from the breeding grounds did not differ between the individuals that failed to breed, bred successfully or those that did not attempt to breed. Meaning, that also after nesting failure, individuals stayed in the Arctic. The reason for staying could be the sufficient levels of resources but also extra time available that they could use for searching a nesting area for the following year.

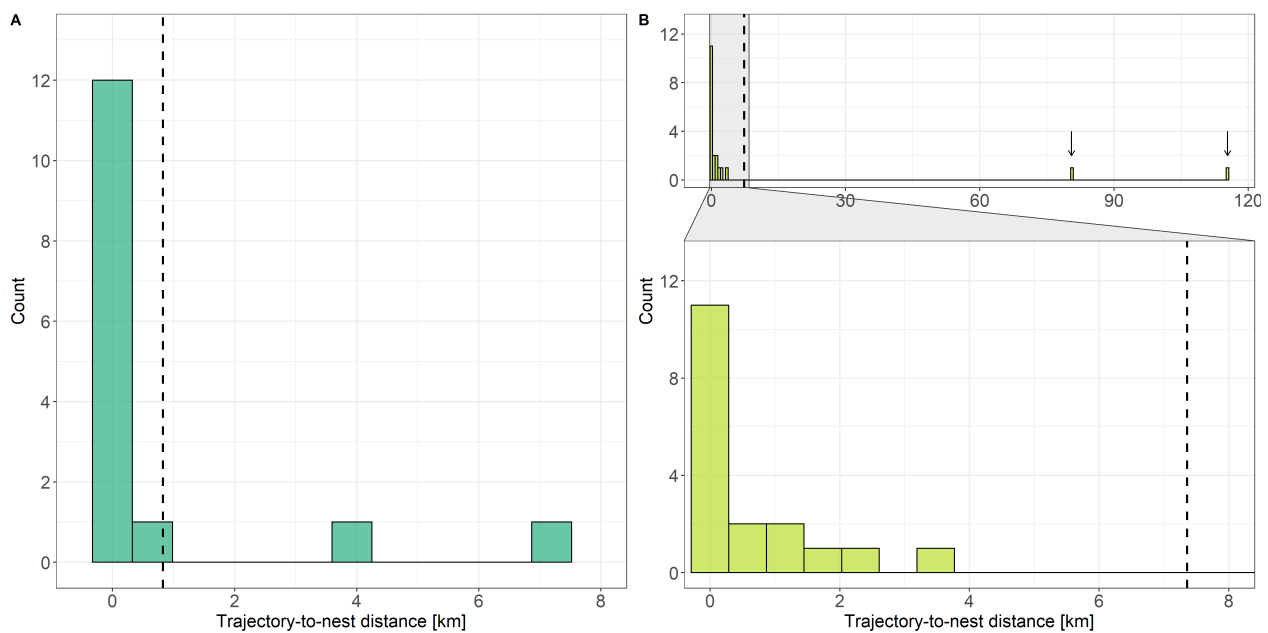


Figure 3.5. Histogram of the minimum distance between the trajectory of the current year and nest location of the following year (trajectory-to-nest distance) for (A) nesting failure and (B) nesting success. Dashed line represents the mean value.

Second, both failed and successful breeders prospected during the post-breeding period. Failed breeders prospected more than successful breeders, likely because they had more time after the failed breeding attempt to explore the area. However, this result could also suggest that failed breeders had more time available to find a suitable nesting area for the following year. The difference in prospecting between the failed and successful breeders was especially evident in areas with variable resources, while the difference in areas with stable resources was smaller. In the models with included MCP and distance from the nest were present spikes on the graph after Julian date 275 for successful individuals (Figure 3.1). These spikes represent individuals that were likely already on migration, meaning that

without these locations included, we would see a somehow smaller increase in prospecting throughout the season. In areas with stable resources, the overall distances covered during prospecting movement were much smaller than in areas with variable resources. A likely explanation is that Kolguyev Island, belonging to the "stable resources" group, is a relatively small island and individuals do not want to cross the water but rather stay on an island until the end of the season. At the same time, the island provides stable resource-rich habitat (Mooij et al. 2011), so individuals do not need to search for an area far away from their initial breeding site.

Third, rough-legged buzzards that failed to breed as well as those that bred successfully returned to the area they explored the year before. Failed breeders were on average closer to the nest of the following year (within 1km) than successful breeders (within 8km). This is because of the two individuals which were moving towards the nest location of the previous year during the spring migration but stopped before the coast (Figure S3.2). The reason could be that they found a suitable nesting area on the way and decided to settle or at the time of arrival to the coast, the wind conditions were not suitable for crossing, so they decided to settle on the mainland. Wind conditions are indeed an important factor when deciding to cross water bodies (Nourani et al. 2016). Yet, in the following years, individuals returned to the same area for breeding (Figure S3.4).

Opposite to our hypothesis presented in Figure 3.1, breeding success did not determine if individuals will return to the same nesting area. In some cases, failed breeders could search for a nest location but afterwards still return to the same area to breed since they did not find a more suitable location. In contrast, successful breeders could during their prospecting movement find a more suitable nesting area and in the following year return to that area for breeding. However, regardless of the breeding success or how much they prospected, rough-legged buzzards bred in the area they have previously surveyed. Next, in this study, we assumed that nesting success depends mainly on resource availability in the breeding area. However, other factors such as landslides, shifts in temperature and heavy rain can cause nesting failure (Bradley et al. 1997, Pokrovsky et al. 2012, Beardsell et al. 2017). In 14 out of 32 cases of nesting failure (44%), for which we had available nesting data, we confirmed (with field observations) that the lack of food was indeed a cause. This is quite a large percentage and we can argue that resource availability is one of the major factors that determine nesting success in rough-legged buzzards. Indeed, density

of rough-legged buzzards was high in the year after the rodent-peak (Pokrovsky et al. 2014) which suggests that nesting success is affected by resource availability. Climate change is however expected to cause more precipitation and higher temperature changes in the future which might cause higher mortality of nestlings (Hanssen-Bauer et al. 2003).

With the global change, also rodent peaks are predicted to become less regular (Kausrud et al. 2008). In several areas across the Arctic, the rodent cycles already started to stagnate (Ehrich et al. 2020). We do not have precise information on rodent cycles for our entire study area but in the areas close to our study sites the cycles are still evident (Ehrich et al. 2020). Yet, in the future, we can expect that with less evident lemming cycles, rough-legged buzzards will likely switch to alternative prey and thus change their movement patterns. We speculate that prospecting movement during the breeding season in failed breeders would become less evident with shorter distances and smaller area covered. This could potentially affect genetic diversity and cause populations to become more isolated as was the case for peregrine falcons (*Falco peregrinus*) Gu et al. (2021).

In summary, we showed that rough-legged buzzards have highly flexible movement and do not follow clear distinct patterns in the case when they breed successfully and when they fail to breed. However, we demonstrated that the prospecting movement during the post-breeding period plays an important role in finding a nesting area for the following year and can determine the fate of nesting. Such a way of dealing with a lack of time and extreme arctic environment suggests that rough-legged buzzards have highly developed spatial memory due to memory-demanding ecological conditions, maybe more than it was previously thought (Pravosudov et al. 2006). We expect that this strategy is used by many migratory species, such as the northern wheatear (*Oenanthe oenanthe*) (Arlt & Pärt 2008), both non-breeders (Doligez et al. 2004, Dittmann et al. 2005) as well as breeders (Forstmeier 2002, Ward 2005) but especially Arctic birds or other animals that face limited time for breeding, fluctuating resources, and harsh environmental conditions. Further studies are needed, to investigate if our results apply to other arctic breeders and to gain more information on how individuals evaluate site quality and how they use environmental cues. Nevertheless, this study provides a step forward towards understanding movement and settlement decisions in animals experiencing changing environmental conditions.

Acknowledgements

We acknowledge the Max Planck Institute of Animal Behavior and the German Aerospace Center (DLR).

Chapter 4

Arctic avian predators synchronise their spring migration with the northern progression of snowmelt

Teja Curk, Ivan Pokrovsky, Nicolas Lecomte, Tomas Aarvak, David F. Brinker, Kurt Burnham, Andreas Dietz, Andrew Dixon, Alastair Franke, Gilles Gauthier, Karl-Otto Jacobsen, Jeff Kidd, Stephen B. Lewis, Ingar J. Øien, Aleksandr Sokolov, Vasiliy Sokolov, Roar Solheim, Scott Weidensaul, Karen Wiebe, Martin Wikelski, Jean-François Therrien, Kamran Safi

Published in *Sci. Rep.* 2020, **10**: 1-11

Abstract

Migratory species display a range of migration patterns between irruptive (facultative) to regular (obligate), as a response to different predictability of resources. In the Arctic, snow directly influences resource availability. The causes and consequences of different migration patterns of migratory species as a response to the snow conditions remains however unexplored. Birds migrating to the Arctic are expected to follow the spring snowmelt to optimise their arrival time and select for snow-free areas to maximise prey encounter en-route. Based on large-scale movement data, we compared the migration patterns of three top predator species of the tundra in relation to the spatio-temporal dynamics of snow cover. The snowy owl, an irruptive migrant, the rough-legged buzzard, with an intermediary migration pattern, and the peregrine falcon as a regular migrant, all followed, as expected, the spring snowmelt during their migrations. However, the owl stayed ahead, the buzzard stayed on, and the falcon stayed behind the spatio-temporal peak in snowmelt. Although none of the species avoided snow-covered areas, they presumably used snow presence as a cue to time their arrival at their breeding grounds. We show the importance of environmental cues for species with different migration patterns.

Introduction

Animals are expected to alter their behaviour as a response to ongoing climate change (Post et al. 2013). Animal movement is a behaviour that can be strongly influenced by external, biotic and abiotic environmental factors (Nathan et al. 2008). Several studies suggested that avian species adjust their movements in response to environmental conditions (Mandel et al. 2008, Tøttrup et al. 2008, Poessel et al. 2018) and consequently, optimise their reproduction and survival (Cox 1985, Alerstam et al. 2003). However, more evidence is necessary to fully understand this mechanism. It is thus important to study individual and species-specific movement responses to the environment, and assess whether these responses differ regarding their spatio-temporal scale (Harel et al. 2016).

Avian migration i.e. seasonal movement between breeding and non-breeding areas is in large part driven by the availability of resources (Newton 2010). Furthermore, the predictability of resources is presumed the main stimulus of migration pattern (Newton 2006, 2012). Ephemeral resources, unpredictable in time and space, can lead to irruptive (facultative) migration, whereas predictable availability of resources is associated with regular (obligate) migration. However, species and populations can display either of these two migration patterns or a mixed migration pattern that combines elements of both behaviours. Depending on the predictability of available resources, arctic-breeding raptor species exhibit contrasting migration patterns, representing a gradient from irruptive, mixed, to regular migration. The snowy owl (*Bubo scandiacus*) is irruptive in parts of its range with a variable migration schedule, and weak fidelity to breeding sites (Newton 2006, Therrien et al. 2014, Holt et al. 2015a, Robillard et al. 2018). The rough-legged buzzard (*Buteo lagopus*) exhibits some flexibility in its migration schedule and site fidelity, but it can occasionally show irruptive movements (Beardsell et al. 2016). The peregrine falcon (*Falco peregrinus*) is a regular migrant that has a fixed migration schedule in combination with high breeding-site fidelity (Fuller et al. 1998, McGrady et al. 2002, White et al. 2002).

Migration patterns in birds are among other factors linked to the predictability of available prey and consequently diet of the species (Alerstam et al. 2003, Robinson et al. 2014). Because prey availability and abundance fluctuates across space and time and differently among prey species (Robinson et al. 2014), diet generalists have a greater chance than specialists to encounter at least some prey types. During the breeding season, the snowy owl is a specialist feeding mostly on microtine rodents (Ferguson-Lees & Christie 2001),

a highly fluctuating food resource (Therrien et al. 2014). The rough-legged buzzard has a mixed diet, specialising on small mammals when available, switching to medium-sized mammals and birds when small mammals are scarce (Ferguson-Lees & Christie 2001, Bechard & Swem 2002, Pokrovsky et al. 2014). The peregrine falcon is a diet generalist, feeding on medium-sized birds, a non-fluctuating resource, but also on small mammals (Bradley & Oliphant 1991, Ferguson-Lees & Christie 2001). Prey availability for the peregrine falcon (a generalist predator) should thus be less variable among years than for the snowy owl (specialist predator) with the rough-legged buzzard in between. While in both irruptive and regular patterns food availability is the ultimate cause for migration, in irruptive migrants it also acts as a proximate stimulus. Irruptive migrants thus respond to local food conditions directly by delaying/advancing migration (Newton 2012), whereas regular migrants should rely less on food conditions but more on proxies such as day length change coupled to a strong endogenous control (Berthold 2001).

The proximate response is especially important during spring migration for migratory species breeding in the Arctic. The window of opportunity with favourable environmental conditions for successful breeding in the Arctic is very narrow and the start of breeding is restricted to a few days only. Arriving at the breeding grounds at the right time is thus crucial for successful reproduction (Bêty et al. 2004, Madsen et al. 2007, Lamarre et al. 2017). While early arrival secures a larger time window for breeding, being too early can expose migrants to harsh weather conditions and low food resources. Migrants should thus adjust their movement during spring migration to arrive at the breeding grounds at the optimal time.

Snow cover can limit access to small mammals at the breeding grounds (Reid et al. 2012, Bilodeau et al. 2013). For this reason, arctic migrants may follow the northern progression of snowmelt during spring migration to optimise arrival time. The snowy owl, being mainly an irruptive migrant and lemming specialist, is expected to closely follow the progression of snowmelt, followed by the rough-legged buzzard and then the peregrine falcon. Arctic migrants may also actively avoid snow-covered areas because of the limited access to small mammals (Sonerud 1986) when they feed during migration (Bildstein 2006). The snowy owl, which relies most strictly on small mammals may exhibit the strongest preference towards snow-free areas, somewhat lower preference is expected from the rough-legged buzzard and the lowest preference from the peregrine falcon. The literature

on this topic is scarce (but see Therrien et al. (2015), Yamaguchi et al. (2017)) and the process of decision-making during migration as a response to snow conditions is largely unexplored. Other environmental factors such as temperature, day length (Bauer et al. 2008), productivity (NDVI - normalized difference vegetation index) (Shariatnajafabadi et al. 2014) and wind conditions (Klaassen et al. 2004, Liechti 2006) were previously described influencing arctic migrants. Here we focus on snow cover as an additional factor that was rarely investigated before and might modulate spring migration movements.

In this study, we assess the impact of snow cover on movements during the spring migration of three top predator species of the tundra. We explore whether they respond differently to the snow cover depending on migration pattern (i.e., irruptive vs regular). First, we investigate whether arctic migrants follow the northern progression of snowmelt and whether the irruptive and regular migrants respond to the snowmelt progression differently. Second, we examine whether they avoid snow-covered areas from alternative options in the environment during the spring migration. We also test whether the avoidance of snow-covered areas differs with the spatio-temporal scale. We predict that (1) irruptive migrants follow the snowmelt the most, regular migrants least, and the effect of snowmelt on migratory movements of mixed migrants should be intermediate; (2) arctic species avoid areas with snow cover, with the irruptive migrants showing the highest and the regular migrants the lowest avoidance, and mixed migrants exhibiting intermediate avoidance.

Methods

Movement data

We used Argos and GPS transmitters deployed from 2001 to 2018 in North America and Eurasia to collect data on three arctic species. We confirm that all experimental protocols were officially approved and all methods were carried out in accordance with the relevant guidelines and regulations. The following boards approved our study: University of Saskatchewan, Animal Protection Committee of Laval University, Animal welfare unit in Norway, Norwegian Environment Agency, USGS Bird Banding Lab, Government of Greenland and The Danish Polar Center, Federal Service for Supervision on Nature Management of Ministry of Natural Resources and Ecology of Russian Federation (Rosprirodnadzor).

Details about permits, capture methods (Bloom et al. 2007), sites and transmitters used are provided in the supplementary material. We removed Argos locations with CLS Argos class lower than 2 (error > 500 meters) (Douglas et al. 2012). We did not filter GPS locations because of their high accuracy (< 100 meters). Since we were specifically interested in spring movement, we extracted spring migration tracks using First Passage Time (see "Determination of spring migration periods" in the supplementary material). After data cleaning, we used 225 individuals that bred in the Arctic for analyses of spring migration, totalling in 245,509 spatial points (Table 4.1, Figure 4.1). Since data were collected as parts of several projects, sampling intervals were not consistent (min = 1 second, median = 6 minutes, max = 39 days). We dealt with these differences by using Step Selection Function (SSF) so that the consecutive positions were separated by a certain threshold value (see below).

Table 4.1. Summary of species, individuals, tracks, days, locations and sampling frequencies included in the study.

Species	Number of ind.	Number of spring migr. tracks	Number of days per track (mean $\pm$ SD)	Number of locs per track (mean $\pm$ SD)	Sampling freq. (min, median, max)
Snowy owl	98	211	37 $\pm$ 35	403 $\pm$ 1008	1 second, 31 minutes, 36 days
Rough-legged buzzard	112	219	72 $\pm$ 54	727 $\pm$ 766	1 second, 2 minutes, 39 days
Peregrine falcon	15	18	32 $\pm$ 21	76 $\pm$ 81	1 second, 8 minutes, 22 days

Data analyses

Environmental variables

We obtained daily snow cover data with a spatial resolution of 500 meters (Global Snow-PackMODIS) from the German Aerospace Center (DLR). The obtained snow-covered data matched the extents and dates of spring migration tracks of the three species (see supplementary material under "Determination of spring migration periods"). This product is based on the daily snow cover products MOD10A1 and MYD10A1 (version 5 and 6 as provided by the National Snow and Ice Data Center NSIDC) of the Moderate Resolution Imaging Spectroradiometer (MODIS), which has been reprocessed to remove the effects of cloud cover and polar darkness (Dietz et al. 2015). Note that after the interpolation process the information about snow cover fraction is lost as only algorithm for interpolating binary snow cover is currently available. Using the R package "raster" (Hijmans 2019b), we

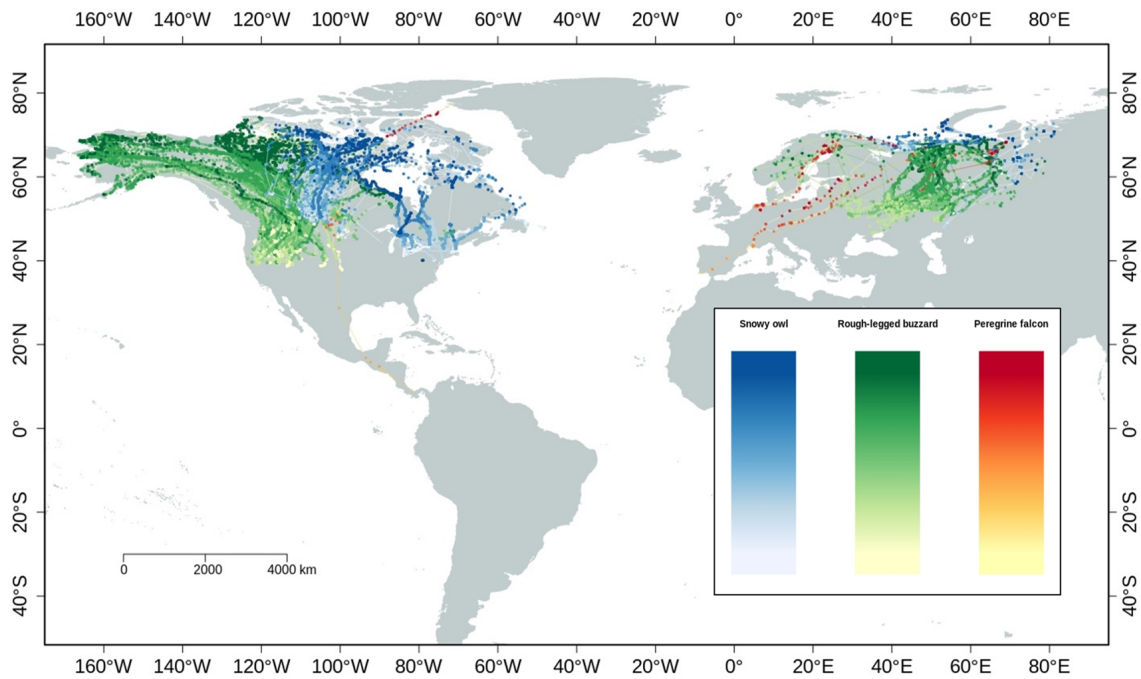


Figure 4.1. Spring migration tracks of the snowy owl, rough-legged buzzard, and peregrine falcon (2001-2018). Colour gradients from lighter to darker tones represent spring dates of migration periods, from earlier to later date respectively.

annotated snow cover values to the modelled movement tracks linking individual locations with snow cover data from the same dates. We calculated day length (hours) using the "daylength" function from the "geosphere" R package (Hijmans 2019a). Through the open-source Env-DATA system (Dodge et al. 2013) we obtained and annotated the following environmental variables: air temperature (°C) at a resolution of 6 hours and 0.75 degrees (ECMWF interim full daily SFC, 2 meters above ground), vegetation index (NDVI) with a resolution of 0.05 degrees and 16 days (MOD13C1) and wind direction variables (U, the east-west component of the wind; V, the north-south component of the wind) with a resolution of 6 hours and 0.75 degrees (ECMWF interim full daily at surface, 10 meters above ground). Based on the U and V components (meters per second), we calculated wind support (wind in the direction of each bird's movement) and crosswind (wind perpendicular to the bird's movement) (Safi et al. 2013), where heading and ground speed were derived from the locations of the individual track.

Step Selection Function

We used Step Selection Function (SSF) to investigate how environmental predictors affect spring movements of arctic raptors (Forester et al. 2009, Potts, Mokross, Stouffer & Lewis 2014, Potts, Bastille-Rousseau, Murray, Schaefer & Lewis 2014, Avgar et al. 2016). The method assumes discrete movement decisions, represented by a fixed time step length. At each step, an animal chooses a location out of a set of available alternate locations characterised by differences in environmental conditions fitted to a conditional logistic regression. We modelled SSFs separately for species and step lengths of one day, three days, and five days to investigate whether decision-making during spring migration changes at different temporal scales ("amt" R package Signer et al. (2019)). Step lengths were chosen so that no auto-correlation of environmental data in time is present (see lags for one - five days in Figure S4.1). We readjusted the data according to the chosen step length so that when two observations were separated by less than the step length value, the second observation was removed, and when two observations were separated by more than the step length value, the later observation was assigned to a different burst. A burst is a segment of a track that includes only locations separated by the chosen step length value. We estimated the distribution of alternative steps using distance and relative angle (angle between the previous and new direction of movement) of the chosen steps within individual migration tracks of each species. Using an exponential distribution, we randomly selected 10 alternative locations for each actual chosen location. These alternative locations together with a chosen location at each step form a stratum. Finally, we annotated chosen and alternative locations with the relevant environmental variables.

Spring movements in relation to the northern progression of snowmelt

We used the chosen locations of individuals at a one-day step length to investigate whether arctic migrants followed the spring snowmelt. We independently tested day length, temperature and NDVI to evaluate whether these factors additionally influence spring movements in arctic migrants. At each location, we extracted snow cover, day length, temperature and NDVI values and compared them between the past, present, and future (from 10 days in the past to 10 days in the future), separately for each species (Figure 4.2a). The scale of 10 days was chosen to exclude possible auto-correlation of environmental data in time (Figure S4.1). Note also that using larger (15 and 20 days) or smaller (5 days)

time-windows resulted in the same overall effect (Figure S4.2). We used generalised linear mixed models (GLMM) implemented in "lme4" (Bates et al. 2015) R packages. In the model, we used snow cover, temperature, day length and NDVI as dependent variables (separately in each model), day as a predictor variable, and year nested in individual as a random effect. We checked the assumptions of the tests and compared models containing all predictors with models leaving out specific predictors to evaluate the effect of each predictor, using Akaike's information criterion (AIC). We considered models with an $\Delta AIC > 2$ as different where the model with lower AIC has stronger support (Burnham & Anderson 2002).

Movement decisions based on snow cover

We compared environmental conditions between chosen and alternative locations (Figure 4.3a) to test whether arctic migrants avoided snow-covered areas when following the receding snow line. In the analysis, we also included wind support and crosswind (only for one-day step length) to test whether these factors would influence the birds' choice of distance and direction and to evaluate whether snow cover predicted movement decisions irrespective of the wind conditions. We fitted mixed conditional logistic regression models using "coxme" function from "coxme" R package (Therneau 2015, Thurfjell et al. 2014), separately by species and separately for one-, three-, and five-day step lengths. As a dependent variable, we included movement decision (chosen vs alternative), as predictors, snow cover, wind support, and crosswind, and as a random effect stratum nested in individual. We performed Shapiro-Wilk's tests for multivariate normality ($p < 0.001$ for each species) and check the test's assumptions. Correlation coefficients between snow cover, wind support, and crosswind were less than 0.7 (Dormann et al. 2013), thus we included these variables in the same model. Based on the Akaike's information criterion (AIC), we compared the full models with those without the predictor of interest to evaluate the effect of this predictor and select a better model. We considered models with an $\Delta AIC > 2$ as different, with lower AIC having more support (Burnham & Anderson 2002). We validated the models with Used habitat calibration (UHC) plots (Fieberg et al. 2018) by comparing the distribution of the observed and predicted values of explanatory variables at the chosen locations with the distribution at alternative locations.

Results

Spring movements in relation to the northern progression of snowmelt

All three species followed the northern progression of snowmelt but responded to snowmelt progression differently. Movements of the rough-legged buzzards were most tightly adjusted to snow progression, those of the snowy owl less, and those of the peregrine falcon the least (see coefficients, SE's and ΔAIC in Table 4.2 and in Table S4.1 and difference in the slopes in Figure 4.2). Higher temperature, longer days and higher NDVI were positively correlated with the spring movements in all three species (see ΔAIC in Table 4.2 and Figure 4.3). For the owl, temperature was the most important factor, following by snow cover, for the buzzard, snow cover was the most important followed by NDVI and for the falcon, temperature was the most important, followed by day length (see ΔAIC in Table 4.2). The species also greatly differed in the snow conditions in the areas they used during spring migration. The owl occurred mostly in snow-covered regions, the buzzard used partially snow-covered areas, and the falcon used snow-free areas (see the snow cover values at day zero; Figure 4.2). This can be seen also with individual migration profiles where responses to snow cover were detected (Figure S4.3). The owl experienced little changes between snow-free and snow-covered areas during migration and continued moving north after entering a snow-covered area. The falcon also experienced little changes between snow-covered and snow-free areas but migrated only when the area was free of snow. The buzzard experienced high variability in the snow-covered and snow-free areas and when it reached the snow-covered area during migration, it waited or retreated to lower latitude before continuing its northward migration.

Movement decisions based on snow cover

The three species did not exhibit any preference or avoidance for snow cover during spring migration when assessing movement decisions at one-day steps (see coefficients, SE's and ΔAIC values on Table 4.3, and slopes on Figure 4.4). At three- and five-day steps, no response to snow cover remained for the three species (see ΔAIC values in Table S4.1). Wind conditions measured at one-day steps, however, influenced their movement decisions. The owl and the falcon moved towards locations with less wind support and the buzzard towards locations with more wind support and crosswind (see ΔAIC values on Table 4.3,

Table 4.2. Snow cover, day length, temperature and NDVI values extracted at each location during spring (at one-day step length) and compared between days (from 10 days in the past to 10 days in the future), separately for each species. Generalised linear mixed models (GLMM) with snow cover, day length, temperature and NDVI as dependent variables (each in a separate model), day as a predictor variable, and year nested in individual as a random effect. To evaluate the effect of the predictor, we compared a model with and without that predictor. Only the results of the full models are presented and those with $\Delta AIC > 2$ are marked with *.

Species (n = number of locations)	Dep. var.	Pred.	Est.	SE	z/t value	p value	ΔAIC	AIC Weight	LL
Snowy owl n = 67572	Snow cover	(Intercept)	1.70	0.51	3.35	<0.001	3461*	1.0	-30794
		Day	-0.10	0.00	-56.70	<0.001			
	Day length	(Intercept)	15.44	0.37	41.64	<0.001	446*	1.0	-181330
		Day	0.05	0.00	21.21	<0.001			
	Temperature	(Intercept)	0.82	1.23	0.67	0.51	4543*	1.0	-224904
		Day	0.30	0.00	68.57	<0.001			
	NDVI	(Intercept)	-0.40	0.05	-7.70	<0.001	3420*	1.0	2472
		Day	0.01	0.00	59.25	<0.001			
Rough-legged buzzard n = 133461	Snow cover	(Intercept)	-1.04	0.15	-7.00	<0.001	8186*	1.0	-72895
		Day	-0.10	0.00	-87.11	<0.001			
	Daylength	(Intercept)	15.44	0.23	67.46	<0.001	501*	1.0	-366250
		Day	0.04	0.00	22.44	<0.001			
	Temperature	(Intercept)	7.07	0.44	15.93	<0.001	6314*	1.0	-417478
		Day	0.20	0.00	80.43	<0.001			
	NDVI	(Intercept)	-0.22	0.02	-11.16	<0.001	7321*	1.0	-42750
		Day	0.01	0.00	86.76	<0.001			
Peregrine falcon n = 6575	Snow cover	(Intercept)	-3.90	1.08	-3.61	<0.001	134*	1.0	-899
		Day	-0.13	0.01	-10.90	<0.001			
	Day length	(Intercept)	16.66	0.83	20.04	<0.001	185*	1.0	-14843
		Day	0.06	0.00	13.76	<0.001			
	Temperature	(Intercept)	6.65	1.76	3.78	0.007	299*	1.0	-17929
		Day	0.13	0.01	17.56	<0.001			
	NDVI	(Intercept)	0.13	0.21	0.63	0.55	107*	1.0	-1079
		Day	0.01	0.00	10.46	<0.001			

and slopes on Figure S4.4). Model validation confirmed the significant effects of wind support and crosswind (see UHC plots in Figure S4.5).

Discussion

Consistent with our first prediction, spring migratory movements of all three arctic raptors we studied were synchronised with the northern progression of snowmelt. In addition to temperature, photoperiod and NDVI, the arctic raptors presumably use also snow cover as a cue during spring migration to avoid arriving too early or too late at the breeding grounds. Indeed, snow cover was the most important predictor for the buzzard, less for the owl and least for the falcon when comparing snow cover with temperature, day length and NDVI. Optimising the timing of arrival allows migrants to find territories rich in resources and to start breeding when conditions are favourable (McNamara et al. 1998, Kokko 1999).

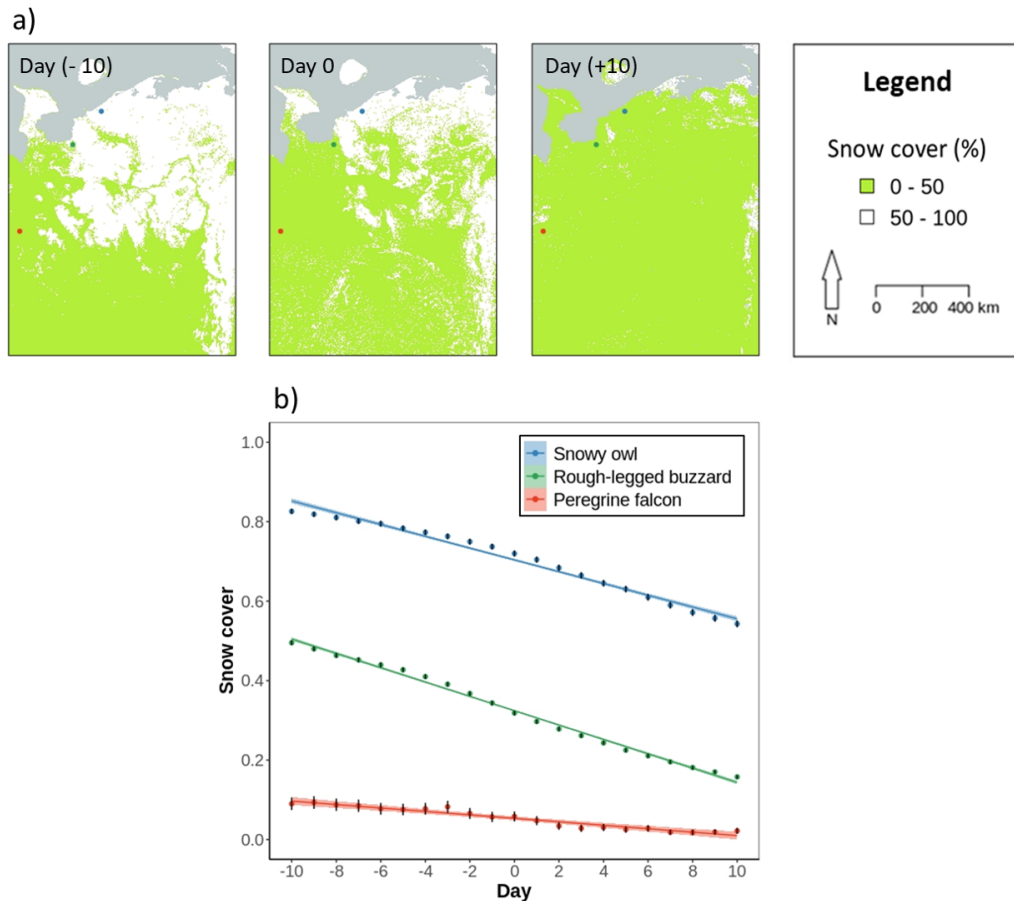


Figure 4.2. (a) Snow cover conditions at the location of snowy owl (blue dot), rough-legged buzzard (green dot), and peregrine falcon (red dot) in 2016 on 2 May (10 days in the past), 12 May (current), and 23 May (10 days in the future). (b) Snow cover conditions (0 = snow absence; 1 = snow presence) at each of the birds' position compared between the days (from 10 days in the past to 10 days in the future) (Table 4.2). Dots with lines represent mean $\pm$ SE of the raw data and shaded areas represent SE of the model estimates.

However, despite the overall trend in following snowmelt progression, our species differed in the details of their responses. We predicted that irruptive species (snowy owl) would track snowmelt most closely, mixed migrants (rough-legged buzzard) would have a weaker association, and that regular migrants (peregrine falcon) would show little association with snowmelt. Consistent with this, the owl and the buzzard were more flexible and followed the snowmelt more than the falcon but surprisingly, the owl responded to the progression of snowmelt less than the buzzard. Perhaps the owl followed the progression of snowmelt by moving to different directions rather than with directed movements. Thus, the pattern of following the northern progression of snowmelt was less evident in the owl than in the buzzard. There is indeed evidence that snowy owls visit and search for suitable areas to

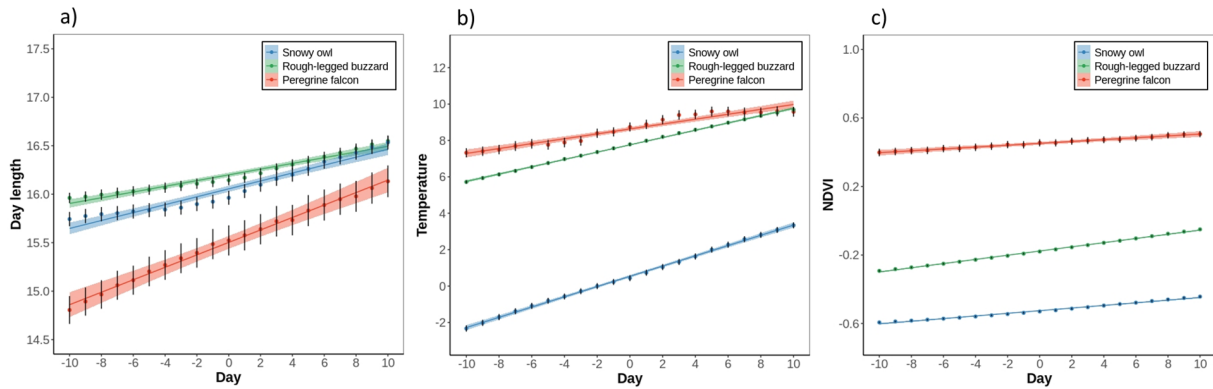


Figure 4.3. (a) Day length (hours), (b) temperature (°C), (c) NDVI (vegetation index from -1 to 1) at each of the birds' position compared between the days (from 10 days in the past to 10 days in the future) (Table 4.2). Dots with lines represent mean $\pm$ SE of the raw data and shaded areas represent SE of the model estimates.

Table 4.3. Movement decisions of arctic raptors according to environmental predictors (snow cover, wind support, and crosswind) at one-day step length. We performed mixed conditional logistic regression models with movement choice (chosen vs alternative locations) as a dependent variable, snow cover, wind support, and crosswind as predictors and stratum nested in individual as a random effect. We performed the models separately by species. To evaluate the effect of the predictor, we compared models with and without that predictor. Only the results of the full models are presented and those with lower AIC and $\Delta AIC > 2$ are marked with *.

Species (n = number of locations)	Pred.	Coef.	SE	z value	p value	ΔAIC	AIC Weight	LL
Snowy owl n = 41316	Snow cover	-0.01	0.04	-0.13	0.90	2	0.3	-35026
	Wind support	-0.05	0.00	-10.99	<0.001	118*	1.0	
	Crosswind	-0.00	0.01	-0.52	0.61	2	0.3	
Rough-legged buzzard n = 72479	Snow cover	-0.05	0.03	-1.88	0.06	2	0.7	-72409
	Wind support	0.01	0.00	2.92	0.004	6*	1.0	
	Crosswind	0.06	0.00	17.02	<0.001	282*	1.0	
Peregrine falcon n = 4147	Snow cover	0.07	0.25	0.29	0.77	2	0.3	-2753
	Wind support	-0.06	0.02	-3.53	<0.001	10*	1.0	
	Crosswind	0.03	0.02	1.78	0.08	1	0.6	

settle and breed during spring migration (Therrien et al. 2014).

While moving to northern breeding sites, the species occupied areas with different snow coverage and thus seemed to follow the northern progression of snowmelt differently. The owl returning to northern breeding areas moved between areas with 75% of snow cover, therefore was ahead of snowmelt. The slow speed of snowmelt in areas the owl passes during the migration can explain our result of an apparent tighter response in the buzzard than in the owl. The buzzard which moved between areas with 35% of snow cover was

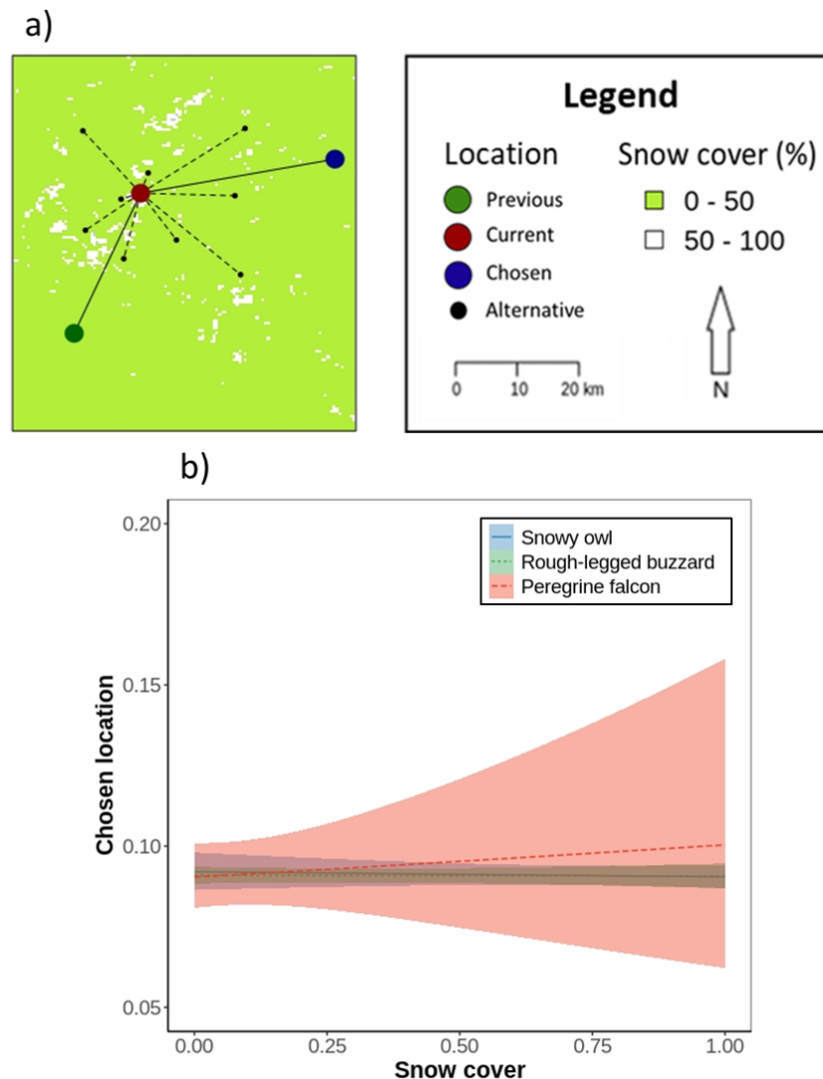


Figure 4.4. (a) An example of the stratum in the step selection function with chosen and alternative locations and the snow cover background. (b) The impact of snow cover (0-snow absence, 1-snow presence) on movement preference (0-alternative vs 1-chosen locations) of arctic raptors during the spring migration at steps separated by one day (Table 4.3). Shaded areas represent SE of the model estimates.

at the peak of snowmelt, passing at the time when snowmelt was most rapid. Indeed, the melt of snow likely follows a sigmoidal curve, slow at first, rapid at 50% snow cover and slow at the end when only patches of snow remain (Kattelman 1991). The buzzard also experienced many changes between snow-free and snow-covered areas which confirms the species being on the peak of snowmelt. In addition, the progression of the buzzard's northern movements was strictly limited by the snow cover in comparison to the other two species which is another reason for the apparent strongest response to snowmelt in this

species. The falcon mostly occupied areas with 10% snow cover and was thus behind the peak of snowmelt. This outcome corresponds to the result that the falcon showed the smallest response to the progression of snowmelt.

Contrary to our second prediction, arctic raptors neither showed a preference nor avoidance for snow-covered areas when following the receding snow line. We predicted that arctic species avoid areas with snow cover, with the owl showing the highest avoidance, the buzzard intermediate avoidance, and the falcon the lowest avoidance. One reason for no response to snow cover could be that the snow cover can represent different conditions of food availability depending on the circumstances. As snow cover affects food availability, the snowy owl and the rough-legged buzzard, which rely on small mammals for food (Ferguson-Lees & Christie 2001), can find prey on snow-free areas (Duchesne et al. 2011). Snow-covered areas might be preferable, given that small mammals are known to concentrate under the snow (Duchesne et al. 2011, Reid et al. 2012, Bilodeau et al. 2013, Domine et al. 2018). As the spring progresses and the snow starts melting, small mammals may not be concentrated under the snow but dispersed, thus the timing in spring could also play a role. Also, physical properties of snow such as depth and density need to be considered when investigating the availability of small mammals in spring (Reid et al. 2012, Domine et al. 2018). In addition, there might be species-specific differences in the preference or avoidance of snow-covered areas depending on their thermoregulation and camouflage requirements (Potapov & Sale 2013).

Other environmental factors additionally influenced the movements of arctic raptors. Besides the northern progression of snowmelt, raptors synchronised their spring migration movements with the increasing temperature, longer days and higher productivity. These environmental factors influenced spring migration timing in several northern migrants, for example, the pink-footed goose (*Anser brachyrhynchus*) (Bauer et al. 2008) and the barnacle goose (*Branta leucopsis*) (Si et al. 2015). When investigating movement preference at each step during the spring migration, movement decisions based on wind conditions differed between the species. The owl and falcon moved towards areas with less wind support while the buzzard moved towards more wind support and crosswind. These results imply that arctic raptors are not necessarily negatively affected by wind support and crosswind and might compensate for the drift similar to the honey buzzard (*Pernis apivorus*) (Klaassen et al. 2010). Wind conditions, thus, seemed to play a secondary role in movement decisions

of arctic raptors.

Our study demonstrates that spatio-temporal changes in snow cover affect the movements of arctic raptors depending on the species differently. The study provides evidence that the species breeding in the same environment and exhibiting contrasting migration patterns respond differently to the snow conditions. Rapid environmental change such as a global increase in temperature is expected to shape snow patterns (Serreze & Barry 2011) resulting in more rapid snowmelt and prolonged snow-free periods (Bhatt et al. 2010). With earlier greening, some species might have broader windows of opportunity for breeding. However, environmental conditions are forecasted to become less predictable too (Post et al. 2009) which represent a challenge for these species. Resulting spatio-temporal changes in food availability (Ims et al. 2008, Kausrud et al. 2008) could force species to alter migration patterns or even strategies (Cotton 2003, Jonzén et al. 2006). The ability of a species to adjust movements to environmental conditions likely depends on the degree of phenotypic plasticity (Charmantier et al. 2008, Switzer 1993). The peregrine falcon, having regular (less flexible) migration would have probably the most difficulty adjusting to changing conditions, which can result in a phenological mismatch (Both et al. 2009, Saino et al. 2010) affecting fitness. In contrast, the snowy owl and the rough-legged buzzard which have more flexible migration, are expected to more easily adapt to these changes.

Changing snow cover patterns caused by climate change will likely shape not only migration patterns of species but have effects that cascade through the entire ecosystem and shape a species' phenology, breeding success, and survival. Thus, at a larger scale, population dynamics, species distribution, and trophic interactions will likely also change (Walther et al. 2002). These changes might occur especially rapidly in the Arctic ecosystem where warming was three times greater than elsewhere over the last three decades (Comiso & Hall 2014, Post et al. 2009). Studying how species track and use the environment is therefore of great importance to predict the impact of future changes. The next step is to model how migration patterns change under different climate scenarios and identify the species in need of management actions. We speculate that our results are applicable to all other irruptive, regular and intermediate migrants in the Arctic but detailed data on the migration patterns of more species are needed to test the applicability of our results. Species might show different responses to the snow cover not only as a result of migration pattern but also due to differences in migration timing and distance, diet, and possibly physical

and physiological adaptation to snow. Although we could not tease apart the potential effects of such variables here, we were able to provide one of the most robust comparisons among species breeding in the same environment. Our study is thus an important step towards understanding the proximate cues that species with different migration patterns use in response to environmental conditions.

Acknowledgements

We thank Risto Karvonen, Arve Østlyngen, Ken Gøran Uglebakken, Dag Gjerstad, Steve Aslaksen, Torkjell Morset, Jostein Sandvik and Ole Andreas Forseth for assistance with catching rough-legged buzzards in Norway. For assistance in the field with catching snowy owls in Norway, we thank Norwegian Nature Inspectorate (SNO) in Finnmark, Fjelltjenesten, Statskog (The State-owned Land and Forest Company) in Troms and Nordland. For helping to trap owls in Canada we thank Dan Zazelenchuk, Marten Stoffel, Mike Blom, Erhard Pletz, Mike Russel and for the help in the eastern part of Canadian Arctic, we thank Audrey Robillard. For assistance in trapping owls in the US we thank Mike Lanzone, Nova Mackentley, Tom McDonald, Chris Neri, Norman Smith, and Matt Solensky. We also thank all Project SNOWstorm (www.projectsnowstorm.org) supporters and collaborators. For fieldwork with rough-legged buzzards and peregrine falcons in Russia, we thank Olga Kulikova. For work on rough-legged buzzards in North America we thank Nina Kidd of Kidd Biological Inc, Travis Booms Alaska Dept of Fish and Game, Bryan Bedrosian of Teton Raptor Center, Neil Paprocki of Univ of Idaho - Moscow, Scott Thomas of Kidd Biological, Inc., Colin Dillingham USFS, Dylan Kesler of Vertebrate Systems LLC and Keith LaSage GeoTrak, Inc. We also thank Anne Scharf and Martina Scacco for the help with data analyses, participants of the IMPRS writing course for revising the manuscript and finally, to anonymous reviewers for constructive comments that substantially improved our manuscript.

Chapter 5

Wing tags severely impair movement in African Cape Vultures

Teja Curk, Martina Scacco, Kamran Safi, Martin Wikelski, Wolfgang Fiedler, Ryno Kemp, Kerri Wolter

Published in *Anim. Biotelem.* 2020, **9**: 1-13

Abstract

Background The use of tracking technologies is key for the study of animal movement and pivotal to ecological and conservation research. However, the potential effects of devices attached to animals are sometimes neglected. The impact of tagging not only rises welfare concerns, but can also bias the data collected, causing misinterpretation of the observed behaviour which invalidates the comparability of information across individuals and populations. Patagial (wing) tags have been extensively used as a marking method for visual resightings in endangered vulture species, but their effect on the aerodynamics of the birds and their flight behaviour is yet to be investigated. Using GPS backpack mounted devices, we compared the flight performance of 27 captive and wild Cape Vultures (*Gyps coprotheres*), marked with either patagial tags or coloured leg bands. **Results** Individuals equipped with patagial tags were less likely to fly, travelled shorter distances and flew slower compared to individuals equipped with leg bands. These effects were also observed in one individual that recovered its flight performance after replacing its patagial tag by a leg band. **Conclusions** Although we did not measure the effects of patagial tags on body condition or survival, our study strongly suggests that they have severe adverse effects on vultures' flight behaviour and emphasises the importance of investigating the effects that tagging methods can have on the behaviour and conservation of the study species, as well as on the quality of the scientific results.

Background

When measuring a phenomenon, the mere process of recording it influences our comprehension of the phenomenon itself (Powell et al. 1998). The rapid development of tracking technologies and miniaturised sensors (bio-logging) allows us to finally answer long standing hypotheses about animal behaviour while providing a fertile environment to tackle novel research questions (Kays et al. 2015*b*). GPS loggers and geolocators record animal movements, accelerometers, cameras and proximity sensors can inform us about detailed behaviours and interactions among individuals and internal sensors such as heart rate loggers can provide information about the animals' physiology. Finally, additional sensors can report on the environmental conditions experienced by the animals, such as temperature, air or water pressure and water depth.

The detail and spatial coverage of these data and the fact that they can be collected remotely from wild free-ranging animals are unprecedented, and impossible to achieve using direct observation (Williams et al. 2020). Therefore the use of bio-logging and especially tracking technology is fundamental for the study of animal movement and pivotal to ecological and conservation research. However, the potential bias caused by the process of data collection has been often underrated.

Researchers are aware that tagging devices might affect the behaviour and survival of animals and more and more studies are suggesting solutions to minimise their effects, despite these being difficult to estimate and account for when interpreting results. Several studies have shown that the behaviour of birds can be affected by the attached devices (Barron et al. 2010, Bowlin et al. 2010, Bodey et al. 2018). A study on migrating birds, highlighted how return rates of individuals carrying geolocators were significantly lower than in the control group (Stutchbury et al. 2009). Devices attached to birds were also shown to negatively influence reproduction, nesting, parental care and survival, to reduce flight speeds (Gessaman & Nagy 1988, Bannasch et al. 1994), and to increase energy expenditure (Barron et al. 2010, Bodey et al. 2018). Some studies demonstrated an extension of the foraging trip duration due to the attached devices (Bodey et al. 2018) whereas (Wanless et al. 1989) reported shorter foraging trips for birds equipped with devices compared to the control group.

These behavioural changes can not only have a negative impact on the reproduction and survival of animals (Bodey et al. 2018), but also bias our understanding of animal behaviour

(Barron et al. 2010). In fact, effects of tagging methods pose, beyond being a concern for animal welfare, a major problem because of their systematic bias on the data. So far, there has been little or no research on how tagging methods affect the movement metrics that we collect and analyse, and on which we base our understanding of the behaviour in a population. Although, the effects of devices on animals are difficult to measure, we need to increase our efforts towards quantifying and understanding them. By underestimating the effects of devices we risk to invalidate the efforts of our research community in studying and preserving animal behaviour, especially in the case of threatened species which are often subjects of movement ecology studies.

The weight of a device, relative to an animal's body weight (a currently accepted upper limit of to date 3% or 5%), is in general the only aspect currently considered in movement ecology studies involving tracking technology or marking methods (Kenward 2002, Portugal & White 2018). Yet, also other aspects, such as device attachment (where and how the device is attached to the animal's body) and device-induced drag, have been shown to affect flight behaviour (Vandenabeele et al. 2012). In order to avoid these negative effects, researchers recommended to minimise the weight and reduce the drag coefficient of the device (Bannasch et al. 1994, Bowlin et al. 2010, Pennycuick et al. 2012, Kay et al. 2019), to use flexible harnesses to reduce injuries for the birds (Barron et al. 2010, Vandenabeele et al. 2013), and to position the devices at the centre of gravity to avoid destabilisation (Wanless et al. 1989, Powell et al. 1998, Vandenabeele et al. 2014).

Patagial tags have been extensively used as markers in the last decades and have played an important role in behavioural studies. However, several studies confirmed adverse effects of patagial tags related to behaviour, nesting success and survival (Brua 1998, Zuberogitia et al. 2012, Trefry et al. 2013). Studies on vultures, suggested that patagial tags might affect the aerodynamics of flight by impacting lift (Botha 2007), which could negatively affect the energetic cost of flight. The severity of these effects also depends on tag material, as plastic tags might lift off the surface of the wing during flight and have a stronger impact compared to softer vinyl tags, which lie flat on the wing (Reading et al. 2015). If the weight and drag of a tag on the wing were problematic *per se*, the way in which anatomic structures of the wing interact during flight makes the exact placement of such a tag even more so. A recent review on proper patagial tag placement highlighted how an incorrect placement of a tag on the patagium can cause injuries and result in the

grounding of vultures (Hirschauer et al. 2019). Most of the vulture populations currently studied are endangered and in dire need of informed conservation action; hence studying their movements while finding the least invasive tagging technique to study their behaviour has become a priority. Researchers recently introduced leg bands as an alternative to patagial tags for individual identification (Hirschauer et al. 2019). In addition to marking methods, researchers use GPS tracking devices to follow individual trajectories and assess habitat use, resource selection and flight performance.

In this study, we compare the impact of patagial tags vs leg bands on the flight performance of an endangered soaring bird species, the Cape Vulture (*Gyps coprotheres*). Specifically, we investigate the effects of tag attachment in wild and captive bred individuals on flight probability, proportion of time spent flying, cumulative distance travelled and ground speed.

Results

Between 2015 and 2019 we used GPS devices to track 27 vultures (14 wild and 13 captive bred) marked them with either patagial tags (15 birds) or leg bands (13 birds). The trajectories of the 27 individuals covered an area between -17° and -32° latitude. Individuals equipped with different tag attachments showed clear differences in the area they covered during the tracking period (figure 5.1). The final data set consisted of 5822 tracking days between April 2015 and November 2019, of which 2292 corresponded to birds equipped with leg bands (1079 of wild and 1213 of captive individuals), and 3530 to birds wearing patagial tags (1870 of wild and 1660 of captive individuals). The average tracking time for the individuals in the study was 2380.1 ± 302.7 h [mean $\pm$ SE; min = 172.5 h, max = 7027.6 h]. The number of segments per day considered in the analysis ranged from 1 to 82 and among all individuals, we recorded 2974 days (51%) in which no flight segment was recorded.

In days when at least one flight segment was recorded, the birds flew only 11.3 ± 0.002 % [mean $\pm$ SE] of their daily tracking time, and covered a daily distance of 70.8 ± 1.2 km flying on average with a daily median ground speed of 6.9 ± 0.05 ms⁻¹. A comparison of the raw data between attachment types and groups showed that the proportion of days with flight and the daily values of proportion of time spent flying, cumulative distance travelled

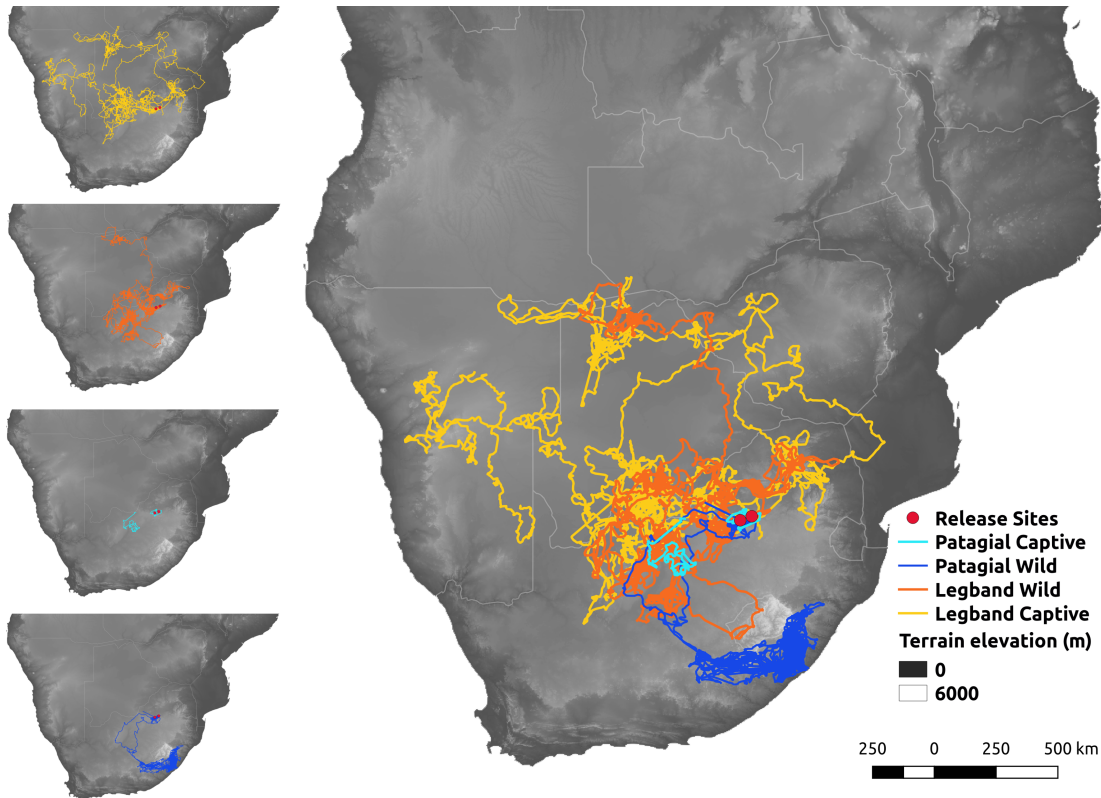


Figure 5.1. GPS trajectories of 27 African Cape Vultures, wild and captive, equipped with either leg bands or patagial tags. Colours show the four combinations of these categories. Red points indicate the release sites.

and median ground speed were the lowest in captive birds equipped with patagial tags and the highest in birds wearing leg bands (similarly so between captive and wild; figure 5.2).

During the study, one captive vulture originally released with a patagial tag was found grounded, whereupon its patagial tag was replaced with a leg band (see Methods). After the tag replacement, we detected an increase in the flight parameters (figure 5.3) for this individual.

Inferences about the effect of tag attachment and group on the flight performance of the birds were drawn based on the results of four generalized additive mixed models (GAMMs). Flight probability, proportion of time spent flying, daily cumulative distance travelled and ground speed were included as response variables. In all four models, attachment type and group (captive or wild) and their interaction term were included as predictors. In order to account for the uneven tracking effort we additionally included the number of daily locations and number of days since release.

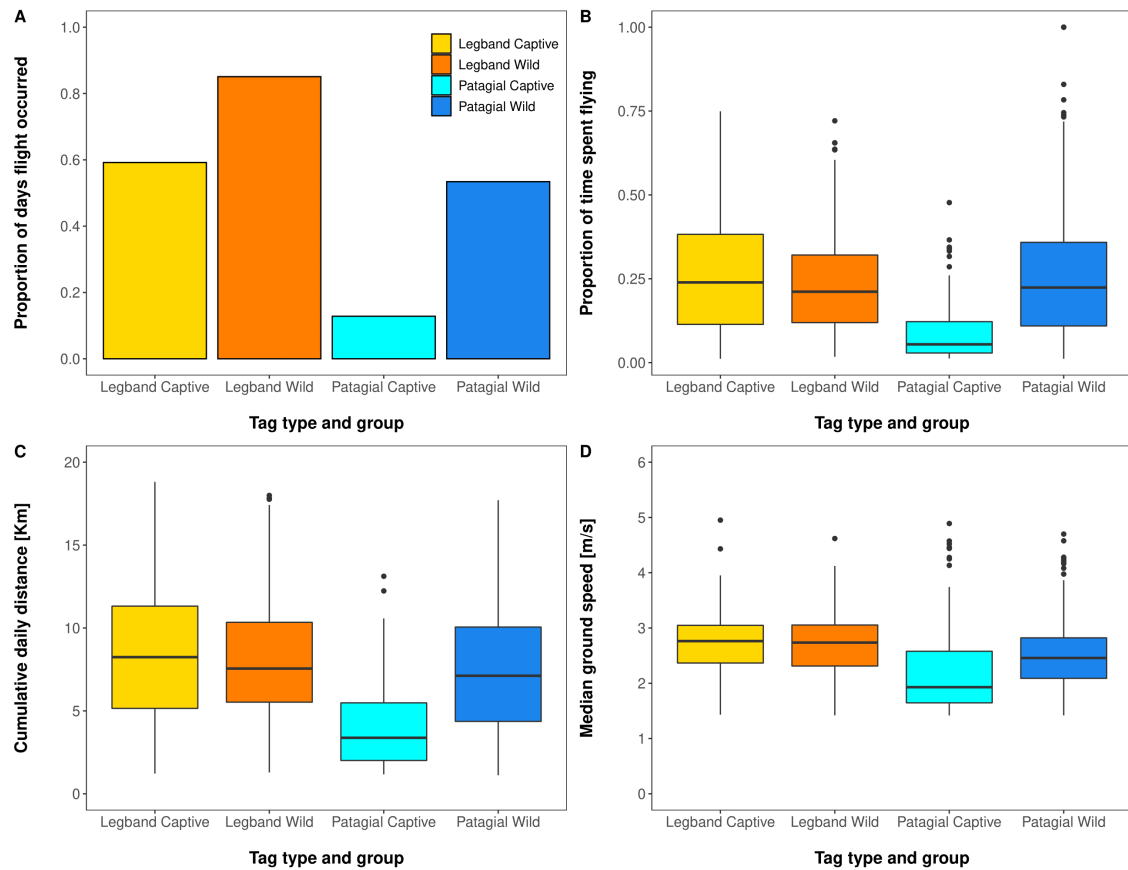


Figure 5.2. (A) Proportion of tracking days in which flight occurred, (B) daily proportion of time spent flying, (C) daily cumulative distance travelled, and (D) daily median ground speed, across groups. Different colours differentiate the four groups: captive bred individuals equipped with leg bands, wild individuals equipped with leg bands, captive individuals equipped with patagial tags and wild individuals equipped with patagial tags.

Occurrence of flight (flight probability)

Occurrence of flight (0 - absence, 1 - presence) was included as a response variable in the first GAMM. This model contained 5822 observations (days) of which 2292 belonged to the leg band group (0 = 656, 1 = 1636) and 3530 to the patagial group (0 = 2318, 1 = 1212), for a total of 27 individuals. The proportion of days in which no flight was recorded was higher for individuals wearing patagial tags (65.6 %) compared to those wearing leg bands (28.6 %; figure 5.2). Our model predicted flight probability to be lower (albeit not significantly) for wild individuals equipped with patagial tags compared to wild individuals equipped with leg bands (patagial = -1.47 ± 0.79 [estimate $\pm$ SE]). The effect of patagial tags on flight probability was the strongest and lower than the significance threshold ($p < 0.05$) for captive individuals equipped with patagial tags (patagial:captive = -2.20 ± 0.83). We detected

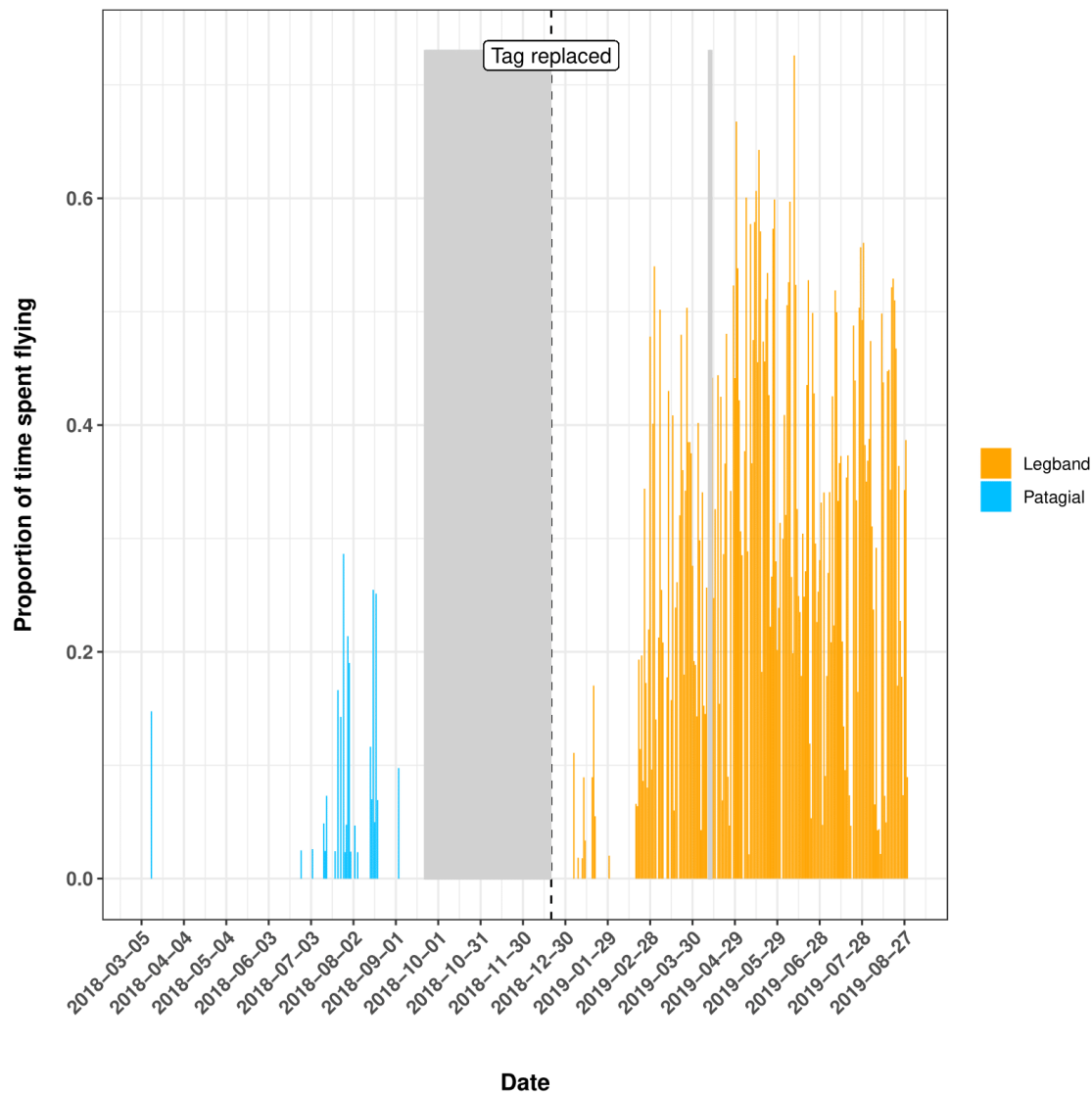


Figure 5.3. Increase in daily proportion of time spent flying for one individual vulture after replacing the patagial tag with a leg band. Days with proportion of time = 0 correspond to days in which no flight occurred. Gray polygons highlight days for which no tracking data were available.

no significant difference between captive and wild individuals equipped with leg bands. Indeed, our model predicted the highest probability to fly (84 %) for wild individuals with leg bands and the lowest (6.47 %) for captive individuals with patagial tags. Among-individual variability was quite high, with 95 % of the individuals having a flight probability between 24.5 % and 98.8 %. However, the variability attributable to individual variation (intercept SD = 1.42) was lower than the effect associated with the patagial attachment both on wild and captive individuals (table 5.1).

Table 5.1. GAMM with occurrence of flight included as dependent variable, interaction between tag attachment and group as fixed term and individual identity as random intercept. Number of days since deployment, number of locations and day of the year were included as smooth terms. The model was fitted with the restricted maximum likelihood using the binomial family and a logit link function.

Coeff.	Est.	SE	t	p
Intercept	1.66	0.59	2.79	**
Patagial att.	-1.47	0.79	-1.86	NS
Captive group	-0.66	0.73	-0.92	NS
Patagial:Captive	-2.20	0.83	-2.65	**
Smooth terms	Edf	Ref. df	F	p
Tracking duration	5.93	5.93	6.62	***
N. Loc.	5.88	5.88	23.35	***
Date	6.75	8.00	13.99	***
Random effects	Intercept Std. Dev.		N. Groups	
Individuals	1.42		27	
N. Observations	5822			
Adjusted R ²	0.30			
NS p>0.05; * p < 0.05; ** p < 0.01; *** p < 0.001				

All smooth terms included in the model - the duration, i.e. the number of days since deployment, number of locations and the Julian date - had a significant effect on the occurrence of flight. Flight probability increased with the number of locations until around 50 locations, indicating that using a number of daily segments < 50 could result in a lower probability of detecting flight. Flight probability was highest ($> 50\%$) between the end of May and the beginning of September (days 150 to 250). The tracking duration (number of days since deployment) positively influenced flight probability after 500 days (about 1.4 years) from deployment (see figure S5.1).

The following three models were all run only on days in which at least one flight segment was recorded ($n = 2848$ days, 1636 corresponding to leg band and 1212 to the patagial group for 27 individuals).

Daily proportion of time spent flying

Daily proportion of time spent flying did not differ significantly for individuals wearing patagial tags, compared to leg bands, nor did it differ between captive and wild individuals. The difference between the groups spending the highest and the lowest proportion of their

time flying was rather small: 0.20 for wild individuals wearing patagial tags (patagial = 0.11 ± 0.14) and 0.16 for captive individuals with patagial tags (patagial:captive = -0.17 ± 0.14). 95 % of the individuals showed a proportion ranging from 0.11 to 0.27, making among-individuals variability high (intercept SD = 0.26) compared to the effect of tag attachment and group (table 5.2).

Table 5.2. GAMM with daily proportion of time spent flying included as dependent variable, interaction between tag attachment and group as fixed term and individual identity as random intercept. Number of days since deployment, number of locations and day of the year were included as smooth terms. The model was fitted with the restricted maximum likelihood using the binomial family and a logit link function.

Coeff.	Est.	SE	t	p
Intercept	-1.51	0.11	-14.23	***
Patagial att.	0.11	0.14	0.77	NS
Captive group	-0.09	0.13	-0.69	NS
Patagial:Captive	-0.17	0.14	-1.20	NS
Smooth terms	Edf	Ref. df	F	p
Tracking duration	7.28	7.28	26.03	***
N. Loc.	8.92	8.92	16584.51	***
Date	7.68	8.00	210.37	***
Random effects	Intercept	Std. Dev.	N. Groups	
Individuals	0.26		27	
N. Observations	2848			
Adjusted R ²	0.93			
NS p≥0.05; * p < 0.05; ** p < 0.01; *** p < 0.001				

Tracking duration, number of daily locations and Julian date, all included as smooth terms in the model, had a statistically significant effect on the proportion of time spent flying. Proportion of time spent flying increased with the number of daily locations and reached its maximum at around 30 locations, indicating that recording < 30 segments per day would decrease our chances to identify flight segments. The model showed a small seasonal effect on the proportion of time spent flying, with a small increase between the beginning of April and the end of October. The proportion of time spent flying did not to be influenced by the duration of the tracking period (see figure s5.2).

Daily distance travelled

Wild individuals equipped with patagial tags travelled significantly shorter distances, of about 10 km less, compared to wild individuals equipped with leg bands (effect size patagial = -0.65 ± 0.22). In captive bred individuals, the difference between distance travelled when wearing leg bands and patagial tags was smaller than in wild individuals (about 7 km) and statistically non-significant. When comparing within the same tag attachment type, we did not find any significant difference between wild and captive bred individuals. The random structure of the model showed small among-individual variation, with 95 % of the individuals travelling between 50 and 72 km/day. The variability attributable to individual variation (intercept SD = 0.37) was lower relative to the effect associated to the patagial attachment on wild birds (table 5.3).

Table 5.3. GAMM with the square root of the daily cumulative distance included as dependent variable, interaction between tag attachment and group as fixed term and individual identity as random intercept. Number of days since deployment, number of locations and day of the year were included as smooth terms. The model was fitted with the restricted maximum likelihood using the gaussian family.

Coeff.	Est.	SE	t	p
Intercept	7.79	0.16	49.42	***
Patagial att.	-0.65	0.22	-2.97	**
Captive group	-0.09	0.21	-0.44	NS
Patagial:Captive	0.19	0.27	0.70	NS
Smooth terms	Edf	Ref. df	F	p
Tracking duration	5.34	5.34	6.37	***
N. Loc.	7.28	7.28	3568.63	***
Date	5.45	8.00	3.76	***
Random effects	Intercept Std. Dev.		N. Groups	
Individuals	0.37		27	
N. Observations	2848			
Adjusted R ²	0.92			
NS p≥0.05; * p < 0.05; ** p < 0.01; *** p < 0.001				

The positive and significant effect of the number of daily locations suggests that collecting a higher number of segments per day would result in recording larger daily distances. Our model showed no seasonal effect on the distance travelled and no increase or decrease in daily movement with the number of days from release (see figure S5.3).

Table 5.4. GAMM with the square root of the daily median ground speed included as dependent variable, interaction between tag attachment and group as fixed term and individual identity as random intercept. Number of days since deployment, number of locations and day of the year were included as smooth terms. The model was fitted with the restricted maximum likelihood using the gaussian family.

Coeff.	Est.	SE	t	p
Intercept	2.67	0.05	58.34	***
Patagial att.	-0.17	0.07	-2.59	**
Captive group	0.02	0.06	0.36	NS
Patagial:Captive	-0.09	0.09	-1.05	NS
Smooth terms	Edf	Ref. df	F	p
Tracking duration	5.60	5.60	7.20	***
N. Loc.	6.30	6.30	85.68	***
Date	4.50	8.00	3.06	***
Random effects	Intercept	Std. Dev.	N. Groups	
Individuals	0.10		27	
N. Observations	2848			
Adjusted R²	0.26			
NS $p \geq 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$				

Daily median ground speed

Wild individuals equipped with patagial tags reached significantly lower ground speeds (about 0.88 ms^{-1} less) compared to wild individuals wearing leg bands (effect size patagial = -0.17 ± 0.07). The model showed no significant differences between wild and captive bred individuals, however the effect sizes suggest that captive individuals wearing leg bands travelled at the fastest speeds, about 7.2 ms^{-1} , while captive individuals with patagial tags at the lowest, about 5.9 ms^{-1} (patagial:captive = -0.09 ± 0.09). Among-individuals variability was relatively high (intercept SD = 0.10) if compared to the largest effect size due to the patagial attachment, and 95 % of the individuals showed a daily median speed between 6 and 8 ms^{-1} (table 5.4).

The number of daily locations, duration of tracking and Julian date significantly influenced median ground speed. Daily median ground speed significantly increased with the number of daily locations and reached an asymptote at around 25 locations. Ground speed also increased until around 200 days (about seven months) after deployment but this increase was not consistent over time. The model also showed a seasonal effect on the daily ground speed, with a slight decrease in speed between the beginning of April and the end of

October (see figure S5.4).

Discussion

We have demonstrated that tag attachment has a severe impact on the flight performance of Cape Vultures. Individuals equipped with patagial tags covered a much smaller area in comparison to the legband group. Our results showed that both wild and captive individuals equipped with patagial tags were significantly less likely to take flight (lower proportion of days in which flight occurred) and when doing so flew at significantly lower ground speed compared to individuals wearing leg bands. Although statistically not significant, we believe it to be relevant that among all groups, captive individuals wearing patagial tags also spent the least proportion of time flying. Finally and as a consequence of the above, our models also showed that wild birds equipped with patagial tags travelled significantly shorter distances compared to those wearing leg bands.

The four groups showed different general directions of movement: individuals in the patagial wild group either remained in the release area or moved towards SE and patagial captive group individuals mainly remained in the release area or moved SSW, while both legband groups showed a movement pattern towards NNW. While the smaller area covered by the patagial groups is in line with our results, there is no obvious hypothesis behind the differences in movement direction observed between groups. However, we could speculate that an interplay of different environmental conditions, including resource distribution and weather conditions, could be the cause of such pattern. Different groups could be attracted to different sources of food, and specific local weather conditions, such as main wind directions at different times and locations, could be guiding the birds to different areas.

Age and experience are known to affect ranging behaviour and distance travelled in vultures, with younger individuals moving more than older ones, who already established their breeding territories (Krüger et al. 2014, Reading et al. 2020). In this study, due to our small sample size, it was not possible to account for age in the models. Our dataset included 21 individuals among which were fledglings, juveniles and subadults and only six adults. However, the adult individuals were equally distributed between the two attachment types, thus we are confident that omitting age from the models did not bias our findings.

Shorter daily distance travelled means smaller area covered every day by the birds to

forage. Vultures are scavengers and as such cover large areas to feed on ephemeral food resources (Ruxton & Houston 2004). At individual and population level, a restricted flight potential and therefore a restricted area available to forage might not be a problem if food resources are abundant, but they surely reduce an individual's ability to react to changes in food availability and environmental conditions. A restricted area covered daily by these birds can also lead to ecosystem-level effects. Scavengers play an important role in the ecosystem thanks to the services they provide, such as preventing the spread of infectious diseases, recycling organic material into nutrients and stabilising food webs (Buechley & Şekercioğlu 2016). Therefore a restricted flight potential and reduction in the area covered by these birds caused by improper tag attachment can have far-reaching consequences at the ecosystem level.

Our results are consistent with previous studies, showing that tag attachment influences foraging trip duration. In some studies, birds carrying extra weight had shorter foraging trips (Wanless et al. 1989, Vandenabeele et al. 2014). Other studies investigating the effect of device weight however showed that birds carrying devices exhibited longer foraging trips (Taylor et al. 2001, Navarro et al. 2008, Bodey et al. 2018), suggesting that individuals wearing extra weight might have to compensate for their increased greater energy demands by travelling more and farther in search for food (Wilson & Wilson 1989, Pennycuik 2008, Vandenabeele et al. 2012, 2014). This might raise questions about whether the decrease in the four flight parameters included in our study should be considered detrimental for the birds. Unfortunately, we did not have access to information about body condition, fitness or survival rate of the individuals after they were tagged. Hirschauer et al. (2019) found that patagial tags can be easily misplaced, and that birds equipped with improperly attached patagial tags were more often found grounded or injured. The results of our study increase the understanding of the effects of patagial tags. By comparing patagial tags and legbands we suggest that patagial tags, even when properly attached, decrease the birds' flight performance, likely increasing the probability of grounding.

All birds included in the study were equipped with a GPS in addition to the marking method (patagial or legband), which might raise concerns in terms of potential cumulative effect of the two devices. Flight parameters from control birds without GPS devices would be difficult to measure and could only be obtained using direct observations. We can therefore only speculate about the cumulative effect of GPS and patagial tags on the flight

performance. However, all birds were equipped with the same type of GPS device and therefore experienced the same additional weight, the only difference being the marking method. This allowed us to estimate the effect of patagial tags on flight performance.

Previous studies suggested that in vultures, a device attached on the wing can influence the aerodynamics of flight (Botha 2007, Reading et al. 2015), while to our knowledge no negative effects on flight performance have been reported for devices attached to the leg. We also presume that patagial tags affect different flight behaviours i.e. soaring, gliding and flapping differently, affecting in particular the gliding phase most severely. Patagial tags may induce a loss of lift by increasing drag. This loss of lift should thus force the birds to increase their air speed to remain aloft, which during gliding they can only achieve by increasing their sinking rate (Pennycuick 2008). Dropping faster will consequently reduce the horizontal distances they can cover while gliding, and eventually result in lower horizontal ground speed, which is what we found in individuals equipped with patagial tags. Smaller distances covered during gliding also result in reduced chances to reach the next available uplift (soaring opportunity) or in the animals misjudging their ability to glide between thermals and thus ground them.

Our suggestion of an adverse effect of patagial tags is further supported by the anecdotal evidence of one individual vulture sequentially equipped with both types of attachment. This captive vulture, originally equipped with a patagial tag and released, was found grounded about 6 months later and after rehabilitation its tag was replaced with a leg band. The data showed that after the tag replacement, all flight parameters measured for this individual increased to match the movement parameters of the other leg banded individuals, suggesting that this individual was rather hampered previously in its movement.

More research is needed to fully understand the consequences of different tagging methods on vultures, including their direct effects on body condition, reproduction and survival. Nonetheless, we urgently recommend using leg bands instead of patagial tags. Should the use of patagial tags be considered unavoidable, we urge researchers to consult experts about the exact positioning of the tag on the patagium (see the manual in Hirschauer et al. (2019)). Some researchers in South Africa already started replacing patagial tagging with leg banding. Fast implementation of such changes, in response to up cutting-edge research on the topic, are especially important for endangered and critically endangered species, such as the Cape Vulture and other African vulture species which are declining in

numbers dramatically (Ogada et al. 2016). In such species, the use of the least invasive tagging method can have a significant impact on their population stability and extinction risk.

Tracking devices and tagging methods are under constant development and the body of literature assessing their impact is inevitably not comprehensive. The challenging task for the movement ecology research community is to keep up with the methodological developments by studying how different devices and attachments affect animal behaviour in order to improve current methods to minimise their impact (Vandenabeele et al. 2013). In addition to reducing the weight of the devices attached on animals, researchers should empirically examine the negative effects of the attached devices, device size and deployment duration on the study species (Portugal & White 2018) and take advantage of the simulation approaches to optimize tag design and reduce drag (Kay et al. 2019). Equipping birds with devices generally affects many aspects of their behaviour and ecology (Barron et al. 2010). In several cases, however, studies reported contradicting results of the effects of different devices on birds (Calvo & Furness 1992, Barron et al. 2010). For example, some studies showed adverse effects of patagial tags while others reported no effects (Calvo & Furness 1992). The reason for that could be that different species respond differently to the attachment of devices because of their ecological differences (Bodey et al. 2018). When assessing which device to use, it is therefore necessary to understand its impacts on the specific study species or on phylogenetically related or functionally similar species. Discrepancies between studies may also be generated by differences in the temporal and spatial scales at which data were collected, or by differences in the environmental conditions the animals experienced (Bodey et al. 2018). Therefore, to gain a better understanding of the impact of tagging methods, it is important to take into account possible differences due to methodology (e.g. tag type, sampling schedule), environmental context (e.g. seasonality), and different aspects of the species' biology (i.e. flight, body condition, reproduction) (Barron et al. 2010, Bodey et al. 2018).

Conclusions

Researchers need to balance the benefits of data acquired by tracking animals with the adverse consequences on the animals' health and the potential biases on the scientific

results. These biases invalidate the comparability of information across individuals and populations tagged with different methods, and defeat the purpose of generalising our behavioural conclusions beyond the single device and attachment. As movement ecologists we aim to study the movement behaviour of animals in different conditions to predict how different species or population would react to changes in their environment. Comparisons at different spatial and temporal scales are therefore an important part of our field of research, but these comparisons risk to become meaningless if we choose to ignore the biases due to how we measure the phenomenon we observe.

Methods

Data collection

Between 2015 and 2019, we tracked 27 Cape Vultures in South Africa (14 males and 13 females of which six were adults, four fledglings, 16 juveniles and one was a subadult). Thirteen vultures were captive bred and 14 wild. We equipped individuals with backpack mounted GPS devices, which were held in place between the shoulders on the bird's back using harness straps that go through the inside of the bird's legs and each collar bone, as described in detail by Wolter and her colleagues (Wolter et al. 2018) (accessible on: <https://vulpro.com/wp-content/uploads/2020/02/Wolter-et-al-Protocols-for-Mass-Capture-Handling-and-Fitting-tracking-devices-on-Gyps-vultures-V3.0-Nov-20181.pdf>). These birds were marked with either patagial tags (56g, figure 5.4A; 15 birds) or a leg band (7g, figure 5.4B; 13 birds). Patagial tags were placed on both wings within the patagium region (Wolter et al. 2018, Hirschauer et al. 2019), while the leg band was fitted only around one leg. Age classes by tag type and group are presented in table S5.1. One individual was released twice, wherefore there are 28 tracking events of 27 individuals included in the study. This captive bred bird was first released on March 5, 2018 and equipped with GPS and patagial tag. On September 21, 2018 the same bird was found grounded and showed no interest in flying. Its patagial tag was removed and the bird was rehabilitated. On December 27, 2018 the bird was equipped with the same GPS model and leg band and released back into the wild. This allowed us to evaluate the effect of the tag replacement on the bird's flight performance.

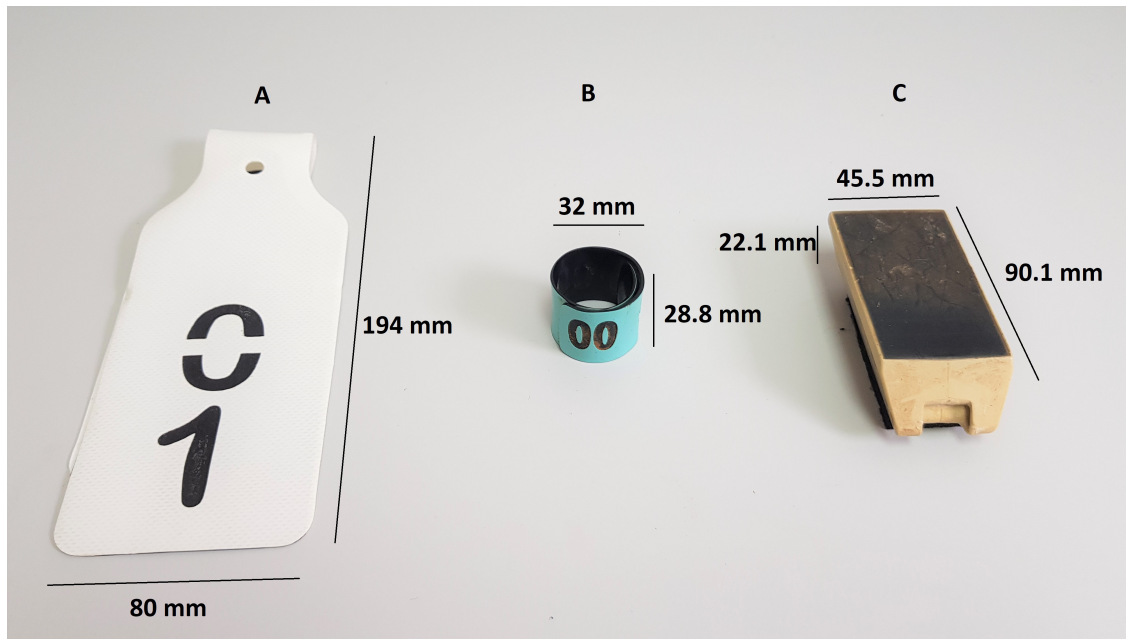


Figure 5.4. Dimensions of (A) patagial tag, (B) leg band and (C) GPS device.

For tracking, we used second and third-generation GPS-GSM Wildlife Telemetry System from Cellular Tracking Technologies (1000-BT3 and 1000a series) with a weight of 68g (90.1 x 45.5 x 22.1 mm; figure 5.4C). The devices sampled positions 24 h/day at the median of either 1, 5 or 15 min. Sampling frequency for some individuals was reduced at night, with 90 % of locations across all individuals being collected between 4:00 and 16:00. The accuracy of the GPS devices was given at 2.5 m (50% CEP statistical test) or 5 m (95 % 2dRMS statistical test).

Captive birds were born and raised in captivity at VulPro's rehabilitation centre and released before the age of one. All wild birds were found grounded due to minor injuries (e.g. heat stroke, starvation, weather) and admitted to the rehabilitation centre at VulPro for a couple of months before being released back into the wild. Before 2018, birds were released from the VulPro rehabilitation centre (long 27.953784, lat -25.710670; captive-bred = 2, wild = 6) whereas after 2018, from the release site located at Nooitgedacht (long 27.535714, lat -25.855547; captive-bred = 11, wild = 8). At both these sites there are established vulture restaurants; however, Kane et al. (2016) found that supplementary feeding sites do not alter the natural foraging behaviours of the Cape Vulture. Furthermore, the two release sites were 60 km apart along with the Magaliesburg mountain range, resulting in birds experiencing the same factors on release, such as the spatial topography, urbanisation,

artificial feeding sites, etc. Therefore, we assume that artificial feeding sites had the same impact on each individual involved in the study.

Data processing

The initial data set included a total of 625,861 GPS locations from 27 individuals and 28 tagging events. We manually removed GPS locations falling outside the African continent. We then removed additional outliers based on speed between consecutive locations using the R package `ctmm` to account for location error (Fleming & Calabrese 2019): we set a conservative GPS error (user equivalent range error) of 10 m, used the functions available in the `ctmm` package to compute speed and variance in speed at each location, and repeatedly removed locations with speed $> 25 \text{ ms}^{-1}$ (Bruderer & Boldt 2001). This procedure was only used to detect and remove outliers but not for statistical purposes. The map in figure 5.1 shows the distribution of the clean trajectories.

After removing outliers we thinned the trajectories, in order to minimise potential biases in speed and distance calculations due to variable sampling frequency. Thinning was done by selecting from the original track only segments with 15 ± 5 min time lag. We then calculated time lag, horizontal displacement (straight-line displacement) and ground speed between locations of the selected segments. Ground speed was calculated as the straight-line displacement between two consecutive locations divided by the time lag. Both thinning and variable calculations were performed using the R package `move` (Kranstauber et al. 2017).

For the next part of the analysis, we excluded segments with variance in speed $> 0.5 \text{ ms}^{-1}$ and time lag > 1 hour because we considered them less reliable in the speed calculation. We classified the remaining segments into flying and not-flying based on a speed threshold of 2 ms^{-1} which we used to calculate metrics of flight performance to evaluate the effects of tag attachment. Specifically, for each individual and day of tracking we calculated: (i) Occurrence of flight (1 if at least one flight segment was recorded in the day, 0 otherwise); (ii) Proportion of time spent flying in a day (sum of flight time divided by tracking time for each day); (iii) Cumulative distance travelled (sum of horizontal displacements during flight segments, in km); and (iv) Median ground speed (median of the speeds achieved during flight segments, in ms^{-1}).

Data analysis

We used four GAMMs (R package `mgcv` (Wood 2003)) to test the effect of tag attachment on each of the above flight parameters. In all four models, attachment type and group (captive or wild) and their interaction term were included as fixed terms. The number of locations and number of days since release (deployment date) were also included in the models to account for the uneven tracking effort (number of locations and tracking duration) between days and individuals. These two parameters were included in the model as smooth terms (thin plate regression splines). Given the year-round tracking, we additionally included in the model Julian date (day of the year in the range 1-366) as cyclic cubic regression spline, to account for non-linear effects of seasonality. Finally, individual identity was included as a random effect in all models. Models including the proportion of time spent flying and occurrence of flight as response variables were fitted as logistic regressions with a "logit" link function. The variables cumulative distance travelled and median ground speed were square-root transformed and the corresponding models fitted using a Gaussian error distribution. Data processing and analysis were performed in R (R Core Team 2019). The complete R scripts to reproduce the analysis can be found in Additional file 2.

Acknowledgements

We would like to thank Alexandra Howard for her contribution in data preparation and the landowners, farmers and volunteers who have assisted us with vulture re-sightings, vulture collections and rehabilitation needs. We would also like to thank two anonymous reviewers for the valuable comments they provided during the revision process.

VulPro would like to thank the following for financial support in making this project and paper possible; Cellular Tracking Technologies, Cheyenne Mountain Zoo, Colchester Zoo, Dallas Zoo, DHL Supply Chain, Hans Hoheisen Charitable Trust, International Association of Avian Trainers and Educators, Max Planck Institute of Animal Behavior, Natural Encounters Conservation Fund Inc. and the Tusk Trust.

General discussion

Main results and conclusions

The results of the first chapter support the “breeding output” hypothesis as an explanation for winter irruptions in snowy owls. Studied individuals were not in a starving condition and their body condition was not different according to the irruption intensity. The causes of irruptions thus seem to lay in a large number of offspring produced when food availability on the breeding grounds is high. Irruptions, at least in some species, might be a strategy to maintain body condition when resource-rich habitats on the breeding grounds become limited due to the large number of individuals and increased competition.

The second chapter supports the idea that resource variability can explain contrasting movement patterns in the snowy owl and that different movement patterns yield the same advantages in terms of resource use. However, the exact mechanism on how individuals move in the environment to secure productive environments while experiencing variable resource predictability, remains unknown. Our individuals did not spend a higher proportion of time in areas with low resource variability as I hypothesized. This suggests that these individuals did not avoid areas with high resource variability but might have adjusted their movement according to the current levels of resources they encountered. These findings are important for understanding the evolution and ecological mechanisms underlying animal movement strategies and for the conservation of the species.

The findings of the third chapter indicate that resource variability and breeding success to some degree affect the movement of the rough-legged buzzards. Individuals who failed to breed prospected more, presumably to find a nesting location for the following year, than individuals that bred successfully. At the same time, buzzards in areas with variable resources prospected more than those in areas with stable resources. However, successful breeders did not mainly return to the same area to breed and failed breeders did not always change the breeding area. Yet, failed as well as successful breeders also returned to the known area for breeding. These results suggest that species that are limited in time, such as the Arctic raptors, developed a strategy of searching for a suitable breeding location for

the following year already during the current breeding season.

The fourth chapter reveals that species with contrasting movement patterns have different proximate responses to environmental conditions. The snowy owl and the rough-legged buzzard adjusted their spring movements to the snow conditions more than the peregrine falcon, however, the snowy owl responded less than the buzzard. Yet, they all followed the northern progression of snow-melt during the spring migration suggesting that they use snow conditions as a cue to time their arrival at the breeding grounds. With this study, I show the importance of environmental cues for species with different movement patterns.

Finally, the findings of the fifth chapter provide evidence that the tagging method affects flight performance in cape vultures. Individuals equipped with patagial tags were less likely to fly, travelled shorter distances and flew slower compared to individuals equipped with leg bands. These results suggest that patagial tags caused adverse effects on the endangered vulture species. This is of great importance for the conservation of the species as well as for the quality of the collected data which can be biased and cause misinterpretation of the observed behaviour.

Implications and future directions

Arctic raptors and environmental change

Each chapter fills a specific gap in knowledge and adds a piece of a puzzle to the bigger picture of understanding the causes, patterns and consequences of movement in animals. Arctic raptors with their tight connection between the movement and environment represent an excellent study system to understand how the environment shapes animal movement. A good example of that is the finding of the fourth chapter which showed that arctic raptors adjust their movements to the snow conditions by following the northern progression of snowmelt during the spring migration.

Future studies should further investigate these tight animal-environment interactions and use the movement of arctic raptors as indicators of environmental change. Specifically, changes in movement patterns in snowy owls found in the second chapter can help us predict changes in environmental conditions. With global climate change, environmental conditions are expected to become less predictable (Post et al. 2009, Verboom et al. 2010) and resulting spatio-temporal changes in resource availability (Ims et al. 2008, Kausrud

et al. 2008) could force species to alter movement patterns (Cotton 2003, Jonzén et al. 2006). Therefore, it seems plausible that strictly nomadic species would be able to adapt to the changed environmental conditions more easily, as compared to strictly regular-migratory species. However, species that exhibit contrasting movement patterns would shift towards nomadism. For example, the peregrine falcon as a regular migrant would have more difficulty adjusting to the new conditions than the snowy owl who can switch to nomadic movement.

In addition, movement decisions within the annual life-cycle are likely to be affected by climate change. With the global increase in temperature, the snow-free period will become longer (Bhatt et al. 2010) and some species might have broader windows of opportunity for breeding. However, climate change can cause a mistiming between the arrival to the breeding grounds and a peak of food availability which can result in population declines (Both et al. 2006). Thus, climate change affects the entire ecosystem by shaping species' phenology, breeding success, and survival and at a larger scale, population dynamics, species distribution, and trophic interactions (Walther et al. 2002). Because these changes occur especially rapidly in the Arctic ecosystem (Comiso & Hall 2014, Post et al. 2009), migratory species that breed in the Arctic are especially in need of a conservation plan.

Patterns of movement

For efficient conservation planning, we need to have knowledge of the species' ecology including movement patterns. The second chapter of this thesis builds upon previous studies by assessing movement patterns at the continuous, rather than discrete scale, which gives us a more precise determination of movement patterns that emerge in animals. Specifically so because some animals exhibit a mixed movement pattern that is not possible to place in a single category. However, the method used in the second chapter is adjusted for the snowy owl study system and thus limited to the continuum between nomadism and regular migration. In further research, this method can be extended to all movement patterns by including different combinations of pairs of movement patterns at the endpoints of the continuum. Still, parameters of the timing of migration and movement distance in NSD profiles should be adjusted to the specific study species. In this way, the unified method for the determination of movement patterns could be developed that can be used in a variety of taxa and thus be comparable across the studies. To investigate whether the results of the

second chapter apply to other species and systems, future studies should include species with a wide range of movement patterns, including residency, regular migration, nomadism, dispersal, and mixed movement patterns at the large spatio-temporal scale.

Causes of movement

Additional studies are needed also to investigate the link between movement patterns and environmental predictability since so far not many studies have addressed this question. There is a need to unify the definition of environmental variability for comparability across studies, as suggested by Riotte-Lambert & Matthiopoulos (2020). With this in mind, also quantification of environmental predictability should be determined so that the predictability estimates can be directly compared between the studies.

In the second chapter, I showed that resource predictability shapes movement patterns in snowy owls and they are able to change between the movement patterns. The sample size was too low to link the changes in movement patterns to the environmental predictability, however, this gap provides an opportunity for future research to investigate the direct factors that influence changes in movement patterns. Movement in animals can be also shaped by anthropogenic factors which we should not neglect when studying animal movement. The example is the fifth chapter which showed that vultures equipped with patagial tags moved significantly less than those wearing leg bends. More similar studies should be performed to understand how anthropogenic factors influence the movement of animals.

Consequences of movement

In this thesis, I did not address the consequences of movement patterns in terms of body condition, reproductive success or survival. Indeed, it would be an interesting topic for further research to measure these parameters and compare them between different movement patterns. Yet, I showed the consequences of movement in terms of resource use i.e. potential for energy intake and demonstrated that the use of resources was comparable between the movement patterns. This study also suggests that there is a trade-off between energy intake and movement, with nomadic species being less efficient. Another example is the first chapter where the results imply that snowy owls move in large numbers (winter irruptions) in order to stay in a good body condition when food resources on the breeding grounds are lacking.

In the fourth chapter, I have shown that species with different movement patterns have different responses to environmental conditions. Rough-legged buzzard with high movement flexibility had a stronger connection to the snow conditions than the less flexible peregrine falcon. This suggests that more flexible, nomadic species gather information from the environment and use environmental cues more than less flexible regular migratory species. With the rapid environmental change, I expect that as species and individuals will become more nomadic, also their cognitive abilities will start to change through generations. The responses to the environment would in an increasing proportion consist of information use from the environment while progressively less from learning and memory (Riotte-Lambert & Matthiopoulos 2020). However, the very high unpredictability of resources that favours strict nomadism should be in large part genetically encoded (Riotte-Lambert & Matthiopoulos 2020). Yet, this expected link between cognitive abilities, environmental predictability and movement patterns should be empirically tested.

Tracking technologies and data acquisition

It would also advance our knowledge to use a combination of different bio-logging data that provide different aspects of information on the animal's state and its environment. In the studies included in this thesis, I used mostly GPS as Argos tracking data with an exception of the third chapter where I included ACC data to estimate nesting success and duration. For example, bio-logging sensors could be used to measure temperature and humidity in combination with high-resolution remote sensing data to gain information on the local environmental conditions an animal is experiencing. In addition, remotely collected data can be complemented with environmental and behavioural data collected from the field for an even more precise estimation of environmental conditions. Finally, further studies should try to test different aspects of movement ecology paradigm (Nathan et al. 2008) within the same study by, for example, investigating environmental conditions but also the physiological state of an individual using implanted data-loggers.

However, it is important to balance the new acquisition of data with data already available, given that attached devices may potentially lead to adverse effects. By using the data that was initially collected for other research questions, we do not only risk causing adverse effects for animals but also save time and resources. Yet, working with such data represents a challenge because the experimental design was not adjusted for our project. Thus, rather

than designing a study for the specific research question we want to answer, we face the challenge of first looking into the data and ask ourselves what research questions can we answer with these data. We should also increase our knowledge on the impacts devices have on the well-being and behaviour of our study species also because equipping animals can introduce bias in the scientific results. Care is needed when studying endangered species and rather than tagging a large number of individuals, in this case, we should use a taxonomically similar species as a proxy to answer our research questions.

Conclusion

In the future, we should continue to investigate how individuals track and use the environment since this knowledge can help us to predict the impact of future environmental change. By increasing our understanding of the impacts of environmental change on the animal movement we will be able to identify the species in need of management actions. As Edward O. Wilson said: "Every species is a masterpiece, exquisitely adapted to the particular environment in which it has survived." This gives us the scientists opportunity to develop exciting research questions and study interesting phenomena such as animal-environment interactions. However, as ecologists, we have the responsibility to not only study what is interesting to us but to choose research questions that will help to preserve biodiversity. Because if not us, who will?

Appendix 1

Supplementary material to Chapter 1 -

Winter irruptive Snowy Owls (*Bubo scandiacus*) in North America are not starving

Teja Curk, Tom McDonald, Dan Zazelenchuk, Scott Weidensaul, David Brinker, Steve Huy, Norman Smith, Trish Miller, Audrey Robillard, Gilles Gauthier, Nicolas Lecomte, Jean-François Therrien

Table S1.1. Model averaging explaining body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) according to day (day of the winter season from 1 October to 1 April) tested separately by sexes in regular (North America Prairies) and irregular (northeastern North America) wintering areas, using linear mixed models fitted with maximum likelihood.

Response variable: Residuals	Predictor variables	Slope	2.5%CI	97.5%CI
Change in body condition of female Snowy Owls throughout winter in regular wintering areas (n = 275)	(Intercept)	80.6	-36.6	197.7
	Day	0.1	-0.7	0.9
	Age class Juvenile	-361.5	-546.6	-176.5
	Age class Juvenile: Day	0.5	-0.2	2.2
Change in body condition of male Snowy Owls throughout winter in regular wintering areas (n = 138)	(Intercept)	53.7	-54.4	161.8
	Day	-0.03	-0.7	0.6
	Age class Juvenile	-193.6	-332.8	-54.5
	Age class Juvenile: Day	0.3	-0.4	1.7
Change in body condition of female Snowy Owls throughout winter in irregular wintering areas (n = 275)	(Intercept)	-134.6	-253.5	-15.6
	Day	1.1	0.3	2.0
	Age class Juvenile	-27.8	-27.8	99.3
	Age class Juvenile: Day	0.2	-0.2	2.1
Change in body condition of female Snowy Owls throughout winter in irregular wintering areas (n = 278)	(Intercept)	-74.8	-177.0	27.5
	Day	1.0	0.4	1.7
	Age class Juvenile	-74.7	-179.8	20.9
	Age class Juvenile: Day	0.1	-0.6	1.4

Table S1.2. Model averaging explaining body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) according to region (regular vs. irregular wintering areas) tested separately by sexes, using linear mixed models fitted with maximum likelihood.

Response variable: Residuals	Predictor variables	Slope	2.5%CI	97.5%CI
Difference in body condition of female Snowy Owls between irregular and regular wintering areas (n = 261)	(Intercept)	-12.1	-90.8	66.6
	Region: West	161.0	73.1	249.0
	Age class Juvenile	-60.0	-137.3	17.3
	Age class Juvenile: Region	-294.5	-404.7	-184.2
Difference in body condition of male Snowy Owls between irregular and regular wintering areas (n = 206)	(Intercept)	12.9	-64.5	90.4
	Region: West	38.9	-63.7	141.4
	Age class Juvenile	-76.0	-163.8	11.8
	Age class Juvenile: Region	-111.3	-239.8	-24.9

Table S1.3. Model averaging explaining body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) according to winter irruption intensity (i.e. Christmas Bird Count (CBC) value given for each winter season) tested separately by sexes, using linear models fitted with maximum likelihood.

Response variable: Residuals	Predictor variables	Slope	2.5%CI	97.5%CI
Effect of irruption intensity on body condition of female Snowy Owls early in the winter in irregular wintering areas (n = 144)	(Intercept)	-24.4	-127.1	78.4
	CBC	-1297.9	-10641.3	6359.9
	Age class Juvenile	-30.6	-184.2	35.8
	Age class Juvenile: CBC	14.3	-17267.9	17541.0
Effect of irruption intensity on body condition of male Snowy Owls early in the winter in irregular wintering areas (n = 127)	(Intercept)	-10.9	-151.0	129.3
	CBC	-1967.5	-17023.8	10430.6
	Age class Juvenile	-52.8	-293.7	37.0
	Age class Juvenile: CBC	3595.4	-412.3	25838.6

Table S1.4. Model averaging explaining body condition index (OLS residuals) of Snowy Owls (*Bubo scandiacus*) according to period (breeding vs. wintering) tested for adult females, using linear mixed models fitted with maximum likelihood.

Response variable: Residuals	Predictor variables	Slope	2.5%CI	97.5%CI
Difference in body condition of adult females between breeding season and early in winter in irregular wintering areas (n = 55)	(Intercept)	54.7	-14.2	123.6
	Period	-20.5	-165.9	-3.9

Appendix 2

Supplementary material to Chapter 2 -

Contrasting movement patterns are the snowy owls' response to difference in resource variability

Teja Curk, Ivan Pokrovsky, Nicolas Lecomte, Tomas Aarvak, Kirk Bates, David F. Brinker, Mark Fuller, Gilles Gauthier, Karl-Otto Jacobsen, Olga Kulikova, Ingar J. Øien, Norman Smith, Roar Solheim, Scott Weidensaul, Karen Wiebe, Martin Wikelski, Jean-François Therrien, Kamran Safi

Method comparison

To validate our method, we compared the classification of movement patterns using visual inspection of NSD profiles with the method by Bunnefeld et al. (2011) and MPM. For both methods, we performed the classification following Bunnefeld et al. (2011) by comparing AIC values between nls models for migration, mixed migration and nomadism. The parameters in the functions were the same for both methods (for parameter values see Methods section). Finally, we compared the classification of movement patterns of the two methods with the visual inspection. When comparing the method by Bunnefeld et al. (2011) with the visual inspection, we counted as a matching case also those which were classified with more than one category (due to AIC difference < 2) when one of the cases matched. For the purpose of direct comparison of MPM method with the visual inspection, we categorised continuous MPM values 0 - 0.33 as nomadism, 0.34 - 0.66 as mixed migration and 0.67 - 1.00 as migration. As a matching case, we also considered values that differed for < 0.05 with the classification results from the visual inspection.

The method by Bunnefeld et al. (2011) matched with the visual inspection in 51% (28 out of 55) of cases. From the cases that did not match visual inspection, 78% (21 out of 27) were misclassified as mixed migrants. The likely explanation is that the function for mixed migration in nls models from Bunnefeld et al. (2011) method is the most flexible and thus adjusts better to the NSD lines, especially when lines curved as plateaus. MPM matched with visual inspection in 93% (51 out of 55).

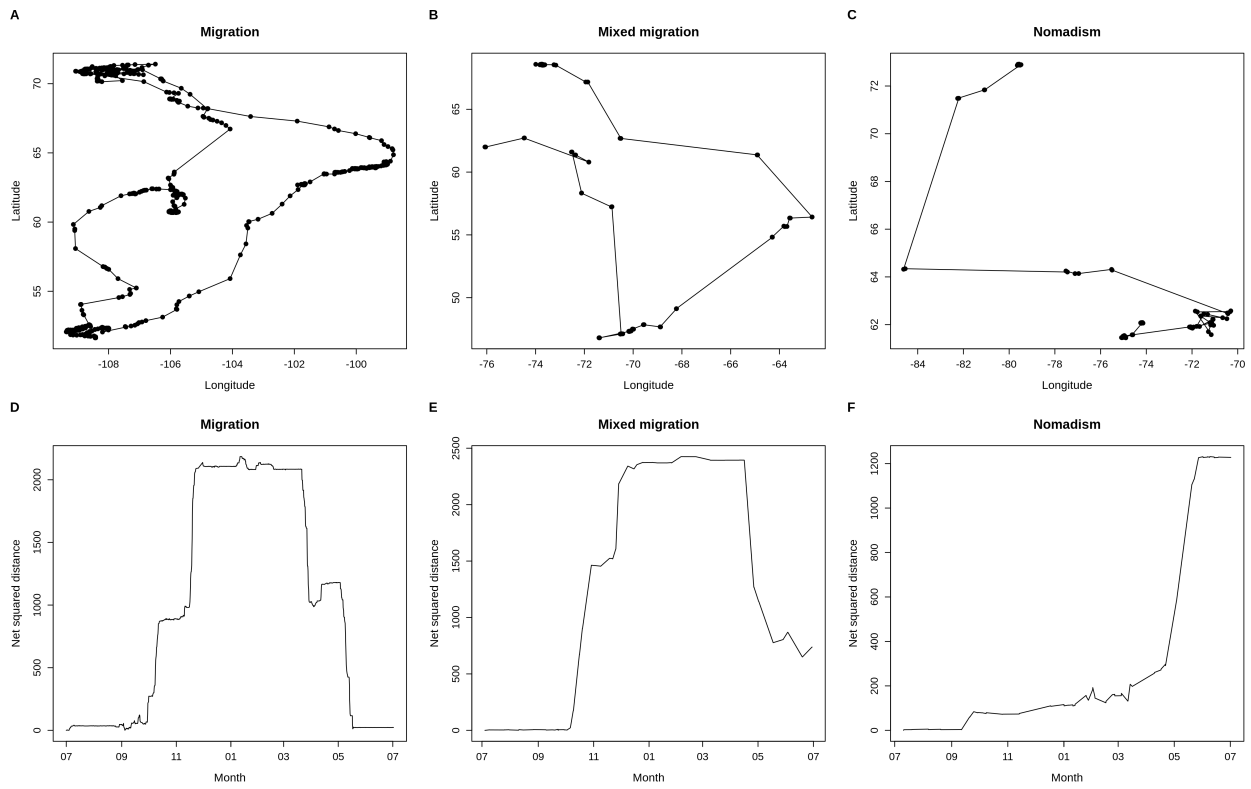


Figure S2.1. Representative trajectories (A, B, C) and NSD profiles (D, E, F) of migration (A, D), mixed migration (B, E) and nomadism (C, F). The MPM values (ranging from 0 to 1) are 0.85, 0.61 and 0.11 for migration, mixed migration and nomadism, respectively.

R code for Migration Pattern Metric (MPM)

```
library (parallel)
library (doMC)
library (plyr)
library (move)
library (PerformanceAnalytics)

#Function for calculating quasi-rsquared value (Spiess and Neumeyer
2010)
quasi.rsq.nls<-function (mdl, y, param)
{
  adj <- (sum(!is.na(y)) - 1)/(sum(!is.na(y)) - param)
  sum.sq <- (sum(!is.na(y)) - 1)    var(y, na.rm = TRUE)
  rsq <- 1 - (adj    (deviance(mdl)/sum.sq))
  return(rsq)
}

#Load a list of individual annual tracks
load("mov_pat.RData")

#Calculate NSD
registerDoMC(detectCores()-1)
E <- llply(1:length(D), .fun=function(i){
  print(i)
  ind1 <- D[[i]]
  ind1 <- ind1[order(ind1$id_ss, ind1$timestamp),]
  move_ind <- move(x = ind1$lon, y = ind1$lat,
    time = as.POSIXct(ind1$timestamp,
    format="%Y-%m-%d %H:%M:%S", tz="UTC"),
    data = ind1,
    proj = CRS("+proj=longlat +ellps=WGS84"),
```

```

        animal=ind1$id_ss)
pts<-coordinates(move_ind)
pt<-as.vector(coordinates(move_ind)[1,])
nsd<-spDistsN1(pts,pt,longlat = TRUE)
ind1$NSD<-nsd
return(ind1)
}, .parallel=T)

```

*#First criteria: run nls models for nomadism and migration following
#Bunnefeld et al. (2010) and calculate quasi-rsquared value*

```

registerDoMC(detectCores()-1)
H <- lply(1:length(E), .fun=function(i){
  print(i)
  nsd <- E[[i]]
  nsd <- nsd[order(nsd$id_ss,nsd$timestamp),]
  nsd$month <- format(as.POSIXct(nsd$timestamp,
                                format="%Y-%m-%d %H:%M:%S"), "%m")
  nsd$julian <- as.numeric(nsd$trans_jul)
  #Model1: Nomadism
  model1 <- tryCatch(nls(NSD ~ beta julian ,
                        data=nsd,
                        start = list(beta=20))
                    ,error = function(e) NULL)
  #Model2: Migration
  model2 <- tryCatch(nls(NSD ~ asym/(1+exp((xmidA-julian)/scale))
                    +(-asym/(1+exp((xmidB-julian)/scale))),
                    data=nsd,
                    start = list(asym=3000,xmidA=105,
                                xmidB=285,scale=5))
                    ,error = function(e) NULL)
  r2_n <- quasi.rsq.nls(model1, nsd$NSD, 1)
  r2_m <- quasi.rsq.nls(model2, nsd$NSD, 1)

```

```

ifelse(identical(r2_m, numeric(0)), r2_m1<-0, r2_m1<-r2_m)
ifelse(identical(r2_n, numeric(0)), r2_n1<-0, r2_n1<-r2_n)
df <- data.frame(id_ss=nsd[1, "id_ss"], r2_nom=r2_n1, r2_mig=r2_m1)
return(df)
}, .parallel=T)

```

```

d <- do.call("rbind", lapply(H, data.frame))

```

*#Second criteria: calculate NSD difference from first to last
#location*

```

dist <- do.call("rbind", lapply(1:length(E), function(i){
  ind <- E[[i]]
  n <- ind[nrow(ind), "NSD"] #last value
  return(n)}))

```

#Normalize the values to get a scale from 0 to 1

```

dist_norm <- do.call("rbind", lapply(1:length(dist), function(i){
  row <- dist[i]
  nor <- (row-min(dist)) / (max(dist)-min(dist))
  return(nor)}))

```

*#Third criteria: calculate the difference between max NSD value
#in winter (Feb-Mar) and summer (Jun-Jul)*

```

slope <- do.call("rbind", lapply(1:length(E), function(i){
  ind <- E[[i]]
  ind <- ind[order(ind$id_ss, ind$timestamp),]
  ind$month <- format(as.POSIXct(ind$timestamp,
    format="%Y-%m-%d %H:%M:%S"), "%m")
  ind$julian <- as.numeric(ind$trans_jul)
  df1 <- subset(ind, julian>214 & julian<243) #values from Feb 1-Mar 1
  m1 <- max(df1$NSD, na.rm = TRUE, finite=TRUE) #max
  df2 <- subset(ind, julian>334 & julian<366) #values from Jun 1-Jul 1
  if(nrow(df2)==0){

```

```

    m2 <- NA
    dif <- NA
  } else {
    m2 <- max(df2$NSD, na.rm = TRUE, finite=TRUE) #max
    dif <- m2-m1
  }
  return( dif )))
anyNA(slope)

#Normalize the values to get a scale from 0 to 1
slope_norm <- do.call("rbind", lapply(1:length(slope), function(i){
  row <- slope[i]
  nor <- (row-min(slope, na.rm=TRUE)) /
    (max(slope, na.rm=TRUE)-min(slope, na.rm=TRUE))
  return(nor) })))
anyNA(slope_norm)

#Add normalized values to the dataset
d$dist_norm<-dist_norm
d$slope_norm<-slope_norm

#Add normalized quasi-rsquared
d$r2_nom_norm <- do.call("rbind", lapply(1:length(d$r2_nom),
  function(i){
    row <- d$r2_nom[i]
    nor <- (row-min(d$r2_nom, na.rm=T)) /
      (max(d$r2_nom, na.rm=T)-min(d$r2_nom, na.rm=T))
    return(nor) })))
d$r2_mig_norm <- do.call("rbind", lapply(1:length(d$r2_mig),
  function(i){
    row <- d$r2_mig[i]
    nor <- (row-min(d$r2_mig, na.rm=T)) /

```

```

    (max(d$r2_mig, na.rm=T) - min(d$r2_mig, na.rm=T))
    return(nor)))
range(d$r2_nom_norm, na.rm=TRUE, finite=TRUE)
range(d$r2_mig_norm, na.rm=TRUE, finite=TRUE)

#Calculate R for criteria 1
r2 <- function(r2_mig_norm, r2_nom_norm) {
  ind <- ((r2_mig_norm + (1-r2_nom_norm))/2)
  return(ind)
}
x1 <- apply(d[,c("r2_mig_norm", "r2_nom_norm")], 1,
  function(x) r2(x["r2_mig_norm"], x["r2_nom_norm"]))
d$r2_joined <- x1
chart.Correlation(d[,c("r2_joined", "dist_norm", "slope_norm")],
  histogram=TRUE, pch=19)

#Join second and third criteria (D and P); NSD difference from
#the first to last point and difference between max values of
#NSD in winter and summer
migr_index_sec_third <- function(dist_norm, slope_norm) {
  ind <- (1-dist_norm) * (1-slope_norm)
  return(ind)
}
ix <- apply(d[,c("dist_norm", "slope_norm")], 1,
  function(x) migr_index_sec_third(x["dist_norm"],
    x["slope_norm"]))
d$dist_joined <- ix
quantile(ix, probs = seq(0, 1, 0.25), na.rm=TRUE)
hist(ix, breaks=15)
chart.Correlation(d[,c("r2_joined", "dist_joined")],
  histogram=TRUE, pch=19)

```

```

#Calculate MPM (all criteria together)
migr_index_final <- function(r2_joined,dist_joined) {
  ind<- (r2_joined + dist_joined)/2
  return(ind)
}
nf <- apply(d[,c("r2_joined","dist_joined")],1,
           function(x) migr_index_final(x["r2_joined"],
                                         x["dist_joined"]))
d$MMP <- nf

```

Appendix 3

Supplementary material to Chapter 3 -

Arctic migratory raptor selects nesting area during the previous breeding season

Teja Curk, Olga Kulikova, Ivan Fufachev, Martin Wikelski, Kamran Safi,
Ivan Pokrovsky

Ethics statement

To carry out the work for this study, Pokrovsky Ivan applied for and obtained permit No. 77-18/0854/4388 from The General Radio Frequency Centre, permit No. RU/2018/406 from Federal Service for Supervision of Communications, Information Technology and Mass Media (Roskomnadzor), and permit No. RU0000045099 from Federal Security Service. No specific permissions were required from Federal Service for Supervision of Natural Resources (Rosprirodnadzor) according to §44 and §6 of the Federal Law of the Russian Federation No. 52 from 24.04.1995 (last update 24.04.2020) 'On Wildlife', and from Federal Service for Technical and Export Control (FSTEC/FSTEK) according to Russian Federation government decree No. 633 from 29.08.2001 and Letter from FSTEK No. 240/33/1373 from 06.04.2015. There were no Special Protected Natural Territories in our study area, and our activities did not include withdrawal of investigated species from nature. In Nenetsky, the work was carried out in agreement with the Nenetsky Nature Reserve in a buffer zone.

Table S3.1. Linear mixed model with departure day as a response variable, year as a fixed effect and bird ID as a random effect. CIs (95%) of predictors were computed by bootstrapping method and 500 simulations using generic R function "confint".

Term	Estimate	Std. Error	lower CI	upper CI	t value	p value
Intercept	269.6	4.9	260.8	278.9	54.3	
year2014	-0.6	5.0	-9.3	8.0	-0.1	0.909
year2015	-0.2	4.9	-9.3	9.1	-0.0	0.975
year2016	11.2	5.3	2.1	20.7	2.1	0.04*
year2017	6.6	5.4	-2.3	16.0	1.2	0.224
year2018	10.2	5.3	0.2	19.1	1.9	0.064.
year2019	6.2	5.5	-3.8	16.0	1.1	0.270
year2020	19.3	6.4	7.1	31.7	3.0	0.005**
Random effects	Variance			Std. Dev.		
Bird ID	48.8			7.0		
Residual	32.5			5.7		
Observations	71					
$N_{individual}$	35					
Marginal R^2	0.27					
Conditional R^2	0.75					

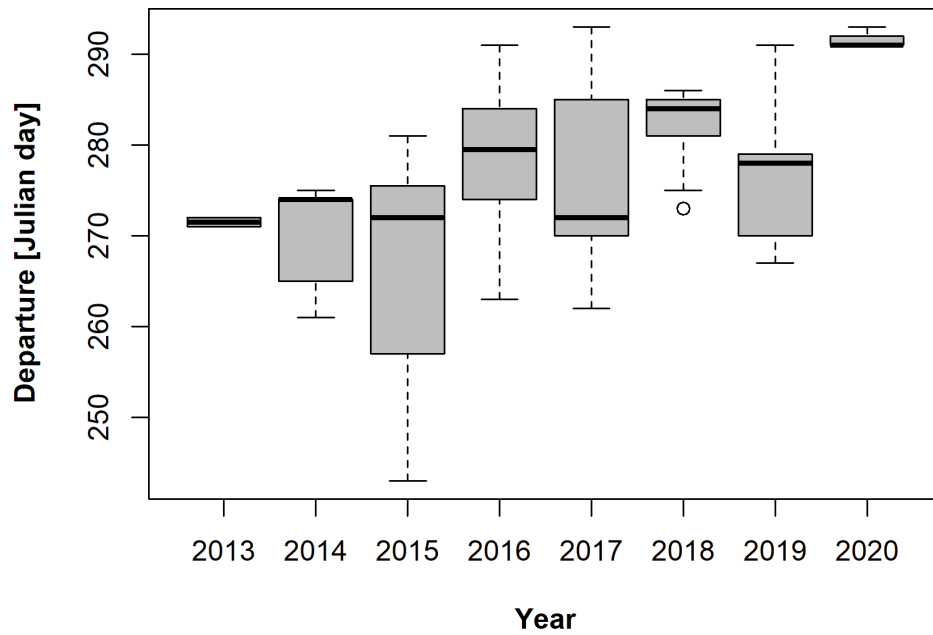


Figure S3.1. Departure day from the breeding grounds as a function of year.

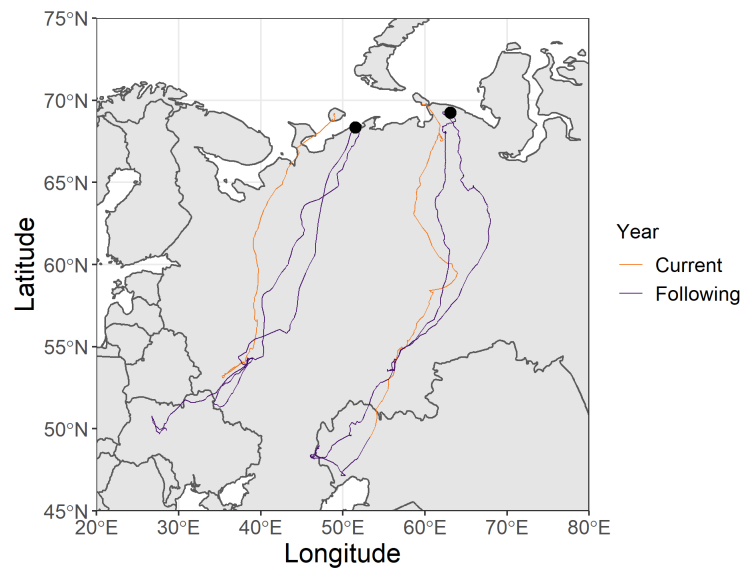


Figure S3.2. Two individual trajectories with distance from the trajectory of the current year and nest location of the following year of more than 15km.

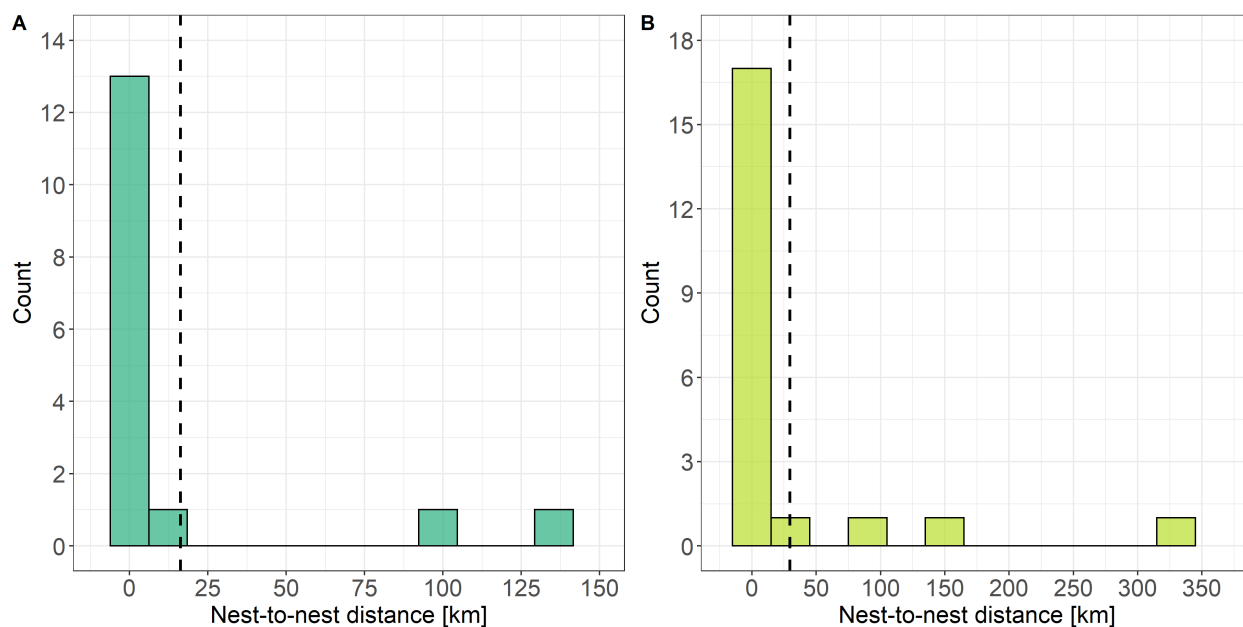


Figure S3.3. Histogram of the distance between the nests of the current and the following year (nest-to-nest distance) for (A) nesting failure and (B) nesting success. Dashed line represents the mean value.

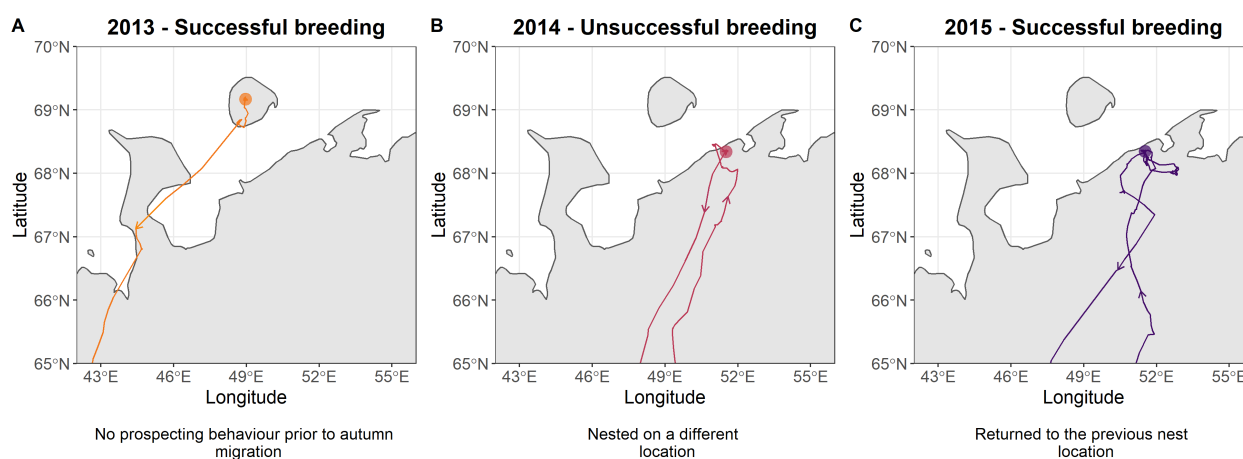


Figure S3.4. Exemplary trajectories of one individual for three consecutive years (A, B, C). Nest locations are marked with dots and arrows represent movement direction.

Appendix 4

Supplementary material to Chapter 4 -

Arctic avian predators synchronise their spring migration with the northern progression of snowmelt

Teja Curk, Ivan Pokrovsky, Nicolas Lecomte, Tomas Aarvak, David F. Brinker, Kurt Burnham, Andreas Dietz, Andrew Dixon, Alastair Franke, Gilles Gauthier, Karl-Otto Jacobsen, Jeff Kidd, Stephen B. Lewis, Ingar J. Øien, Aleksandr Sokolov, Vasiliy Sokolov, Roar Solheim, Scott Weidensaul, Karen Wiebe, Martin Wikelski, Jean-François Therrien, Kamran Safi

Data collection

Snowy owls in western Canadian Arctic

Locations: Areas between Kyle and Saskatoon (Saskatchewan, Canada), Peace River area (Alberta, Canada)

Capture methods: Bal-chatri, remote control released bow-net trap or bal-chatri trap with pigeon or hamster as a lure during wintering

Transmitters used: GPS-GSM transmitters (Ecotone Telemetry, model Saker H, 25 g), Geo-Trak 30g battery ARGOS PTT, Microwave 30g GPS Solar ARGOS PTT

Permits: Animal Care permit from the University of Saskatchewan (number 20090025); banding permits 10736 and 10737

Snowy owls in eastern Canadian Arctic

Locations: Bylot Island, Nunavut in 2007 (n = 12) and 2014 (n = 10), Mary River, Nunavut in 2011 (n = 1) and Deception Bay, Nunavik, QC in 2013

Capture methods: Bow-nets positioned over the nest and bal-chatri

Transmitters used: ARGOS satellite transmitters (Microwave telemetry, USA, PTT-100, n = 14; North Star Science and Technology, LLC, USA, PTT-30G, n = 17)

Permits: Work was conducted under approval from CPAUL (Comite de Protection des Animaux de l'Universite Laval)

Snowy owls in the United States

Locations: North Dakota, Maine, Maryland, Michigan, New York, Pennsylvania

Capture methods: Bow-nets and bal-chatri

Transmitters used: Cellular Tracking Technologies (USA; GSM-Gen2)

Permits: USGS Bird Banding Lab Permits

Snowy owls in Norway

Locations: Troms and Finnmark County

Capture methods: Bow-net (2011 and 2015), and metal grid with multiple nooses (2007)

Transmitters used: Microwave Telemetry 35 g solar PTT (2 females), Microwave 35 g battery powered PTT (2007), Microwave Telemetry 30 g solar GPS PTT (3 ind.), Geo-Trak 30 g battery PTT (2011), Microwave Telemetry 30 g solar GPS PTT (4 ind.), Geo-Trak 30 g battery PTT (2015)

Permits: Permission for catching and instrumenting snowy owls in Norway provided from Animal welfare unit in Norway: 2007-2008 (FOTS ID 209), 2011-2012 (FOTS ID 3346), 2015-2016 (FOTS ID 7561) and from Norwegian Environment Agency: 2007 (2007-6268 ART-VI-ARES), 2011-2015 (2011-3906 ART-VI-ORD).

Rough-legged buzzards in North America

Locations: Rankin Inlet, Nunavut (Canada); Peace River, Alberta (Canada); Alaska, California Nevada, Washington, Idaho, Utah, Montana, Wyoming (USA)

Capture methods: Bal-chatri with house mouse (*Mus musculus*)

Transmitters used: Ecotone 22g solar GPS GSM saker H, Microwave telemetry inc 22 and 30g GPS ARGOS PTT, Geotrak 22g GPS argos PTT

Permits: USGS Bird Banding Lab Master Permit number 22951

Rough-legged buzzards and peregrine falcons in Russia

Locations: Kolguev Island (rough-legged buzzard and peregrine falcon), Nenetsky Ridge (rough-legged buzzard), Vaigach Island (rough-legged buzzard)

Capture methods: Bow-net and Clap-Net Trap on the nest

Transmitters used: E-obs GPS-GSM 43 g for the rough-legged buzzard and E-obs GPS-GSM 25 g and University of Konstanz GPS-GSM 15 g for both rough-legged buzzard and peregrine falcon.

Permits: No specific permissions were required according to the §44 and §6 of the Federal Law of the Russian Federation No. 52 from 24.04.1995 (last update 03.08.2018) â€œOn Wildlifeâ€ to carry out the work for this study. There were no Special Protected Natural Territories in our study area, and our activities did not include withdrawal of investigated species from nature. In Nenetsky, the work was carried out in agreement with the Nenetsky Nature Reserve in a buffer zone.

Peregrine falcons in Russia - Yamal

Locations: Erkuta field station, Yamal Peninsula (68.2° N, 68.9° E)

Capture methods: Noose carpet

Transmitters used: 18g solar PTTs (Microwave Telemetry Inc., MD, USA)

Permits: During the project "Peregrine falcons of the Russian Arctic" (2008-2013) Institute of plant and animal ecology UB RAS applied for and obtained permits from the Federal Service for Supervision on Nature Management of Ministry of Natural Resources and Ecology of Russian Federation (Rosprirodnadzor), Federal service of custom and Export Control and Border service of Federal security service (FSB) to trap, take blood samples and deploy harness-mounted satellite-received transmitters on Peregrine Falcons as well as permissions for researchers to enter the border zone of Russian Federation.

Peregrine falcons in North America

Locations: Centered around the Thule Air Base area (within 100 km), northwest Greenland (76.5° N, 68.7° W)

Capture methods: Harnessed pigeon, noose carpets, and Dho-gaza net

Transmitters used: Microwave Telemetry, 20g Argos PTT, North Star Telemetry, 20g Argos PTT

Permits: Permit to conduct scientific research in Greenland issued by the Government of Greenland and The Danish Polar Center

Determination of spring migration periods

We determined spring migration periods for each individual track using First Passage Time (FPT) following (Fauchald & Tveraa 2003) and (Le Corre et al. 2014). FPT is the time it takes for an animal to cross a circle of a given radius (Johnson et al. 1992). Here, low FPT values correspond to travelling between the wintering and breeding sites, while high FPT values correspond to staying on the wintering or the breeding site. For calculating FPT, we used R package "adehabitatLT" (Calenge 2006b). First, we empirically assessed the radii sizes separately for each species following (Fauchald & Tveraa 2003). We assessed 100 radius values ranging from 1000 to 10000 meters. For each radius and migration track, we

calculated the FPT variance and then we calculated the mean variance per radius. We used the maximum value of the log-transformed mean FPT variance per track plotted against radius to select the radius value (one value per species) in the calculations of FPT of each individual track. Second, we segmented FPT profiles (plotted FPT values against the time of each migration track) by identifying changes in mean and variance using R package "changept" (Killick & Eckley 2014). We then segmented tracks to migration and breeding periods at the breakpoints of mean and variance of FPT profiles. We classified periods of FPT less than five days as travelling, between five and 30 days as searching and more than 30 days as stationary. We defined spring migration periods between the first and last day as travelling, before searching or settling at the breeding grounds. Individual FPT profiles were inspected manually to assure the relevant selection of spring migration periods.

Table S4.1. Binomial mixed models with snow cover as a dependent variable, interaction between day and species as a predictor variable, and individual or year as a random effect. To evaluate the effect of the predictor, we compared a model with and without species included as predictor. Only the results of the full models are presented and those with lower AIC and $\Delta AIC > 2$ are marked with *.

Dep.var. n = number of locations)	Fixed eff.	Random eff.	Est.	SE	z value	p value	ΔAIC	AIC Weight	LL
Snow cover n = 207608	(Intercept)	Individual	-3.45	0.53	-6.55	<0.001	42*	1.0	-108111
	Day		-0.13	0.01	-10.85	<0.001			
	Spec. RL		2.37	0.56	4.20	<0.001			
	Spec. SO		4.86	0.59	8.23	<0.001			
	Day:Spec. RL		0.03	0.01	2.80	0.004			
	Day:Spec. SO		0.03	0.01	2.91	0.005			
Snow cover n = 207608	(Intercept)	Year	-2.33	0.46	-5.06	<0.001	23526*	1.0	-116280
	Day		-0.13	0.01	-11.64	<0.001			
	Spec. RL		2.98	0.97	39.60	<0.001			
	Spec. SO		4.43	0.08	58.68	<0.001			
	Day:Spec. RL		0.05	0.01	4.12	<0.001			
	Day:Spec. SO		0.05	0.01	4.45	<0.001			

Table S4.2. Movement decisions of the snowy owl and rough-legged buzzard according to snow cover at three- and five-day step length. We performed mixed conditional logistic regression models with movement choice (used vs alternative locations) as a dependent variable, snow cover as a predictor and stratum nested in individual as a random effect. We performed models separately by species. To evaluate the effect of each predictor, we compared models with and without the predictor. Only the results of the full models are presented.

Step lengt	Species (n = number of locations)	Pred.	Coef.	SE	z value	p value	ΔAIC	AIC Weight	LL
Three-day	Snowy owl n = 15323	Snow cover	-3.45	0.53	-6.55	0.30	1	0.4	-11986
Three-day	Rough-legged buzzard n = 22583	Snow cover	0.01	0.05	0.27	0.80	2	0.3	-20300
Three-day	Peregrine falcon n = 1276	Snow cover	0.28	0.38	0.75	0.47	1	0.3	-693
Five-day	Snowy owl n = 8316	Snow cover	-0.03	0.09	-0.36	0.72	2	0.3	-5836
Five-day	Rough-legged buzzard n = 12100	Snow cover	0.05	0.07	0.76	0.45	1	0.3	-10166
Five-day	peregrine falcon n = 550	Snow cover	-0.08	1.33	-0.06	0.95	2	0.3	-277

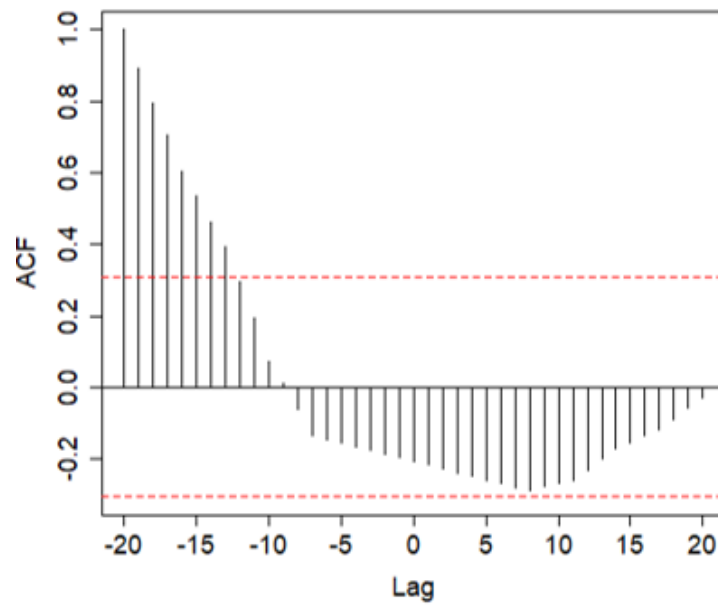


Figure S4.1. Auto-Correlation Function (ACF) of snow cover at time-lag -20 to 20 days for a rough-legged buzzard on May 12, 2016. Red lines represent 95% confidence interval. Note that auto-correlation is only significant for -20 to approximately -10 days.

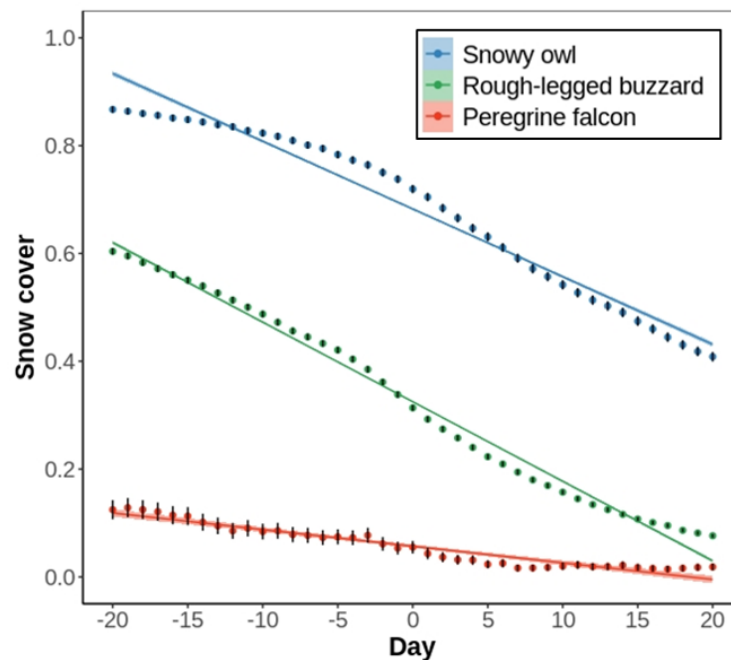


Figure S4.2. Snow cover conditions (0 = snow absence; 1 = snow presence) at each of the birds' position compared between the days (from 20 days in the past to 20 days in the future). Dots with lines represent mean $\pm$ SE of the raw data and shaded areas represent SE of the model estimates.

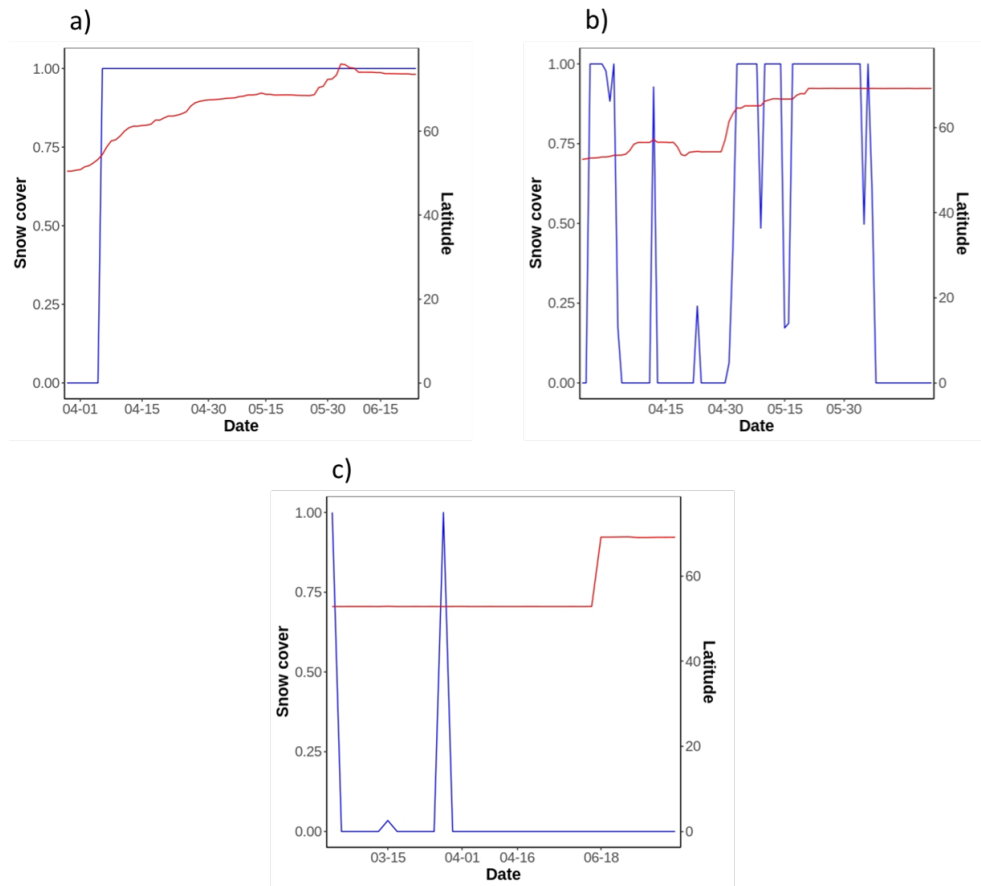


Figure S4.3. The individual response of the snowy owl (a), rough-legged buzzard (b) and the peregrine falcon (c) to the snow cover when moving northward during spring migration.

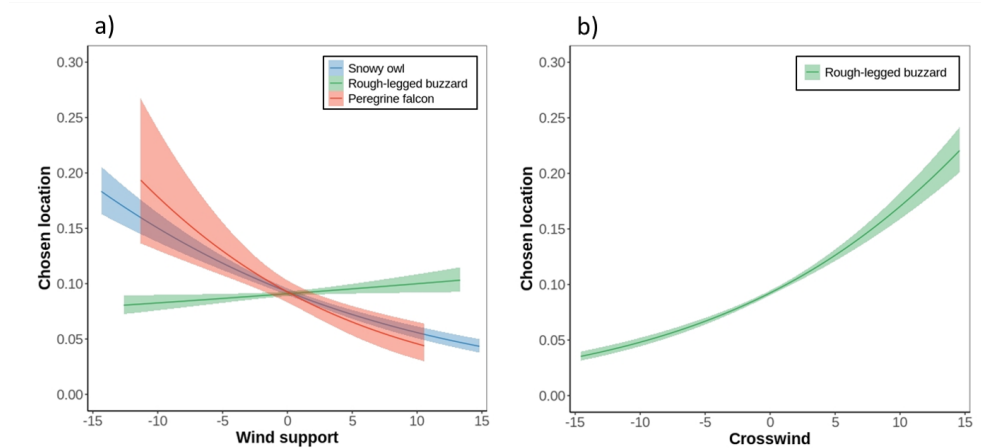


Figure S4.4. Mixed conditional logistic regression models estimating (a) the impact of wind support and (b) the impact of crosswind (m/s) on movement decisions (0-alternative vs 1-used locations) at one-day step length (Table 3). Shaded areas represent standard error. Shaded areas represent SE of the model estimates.

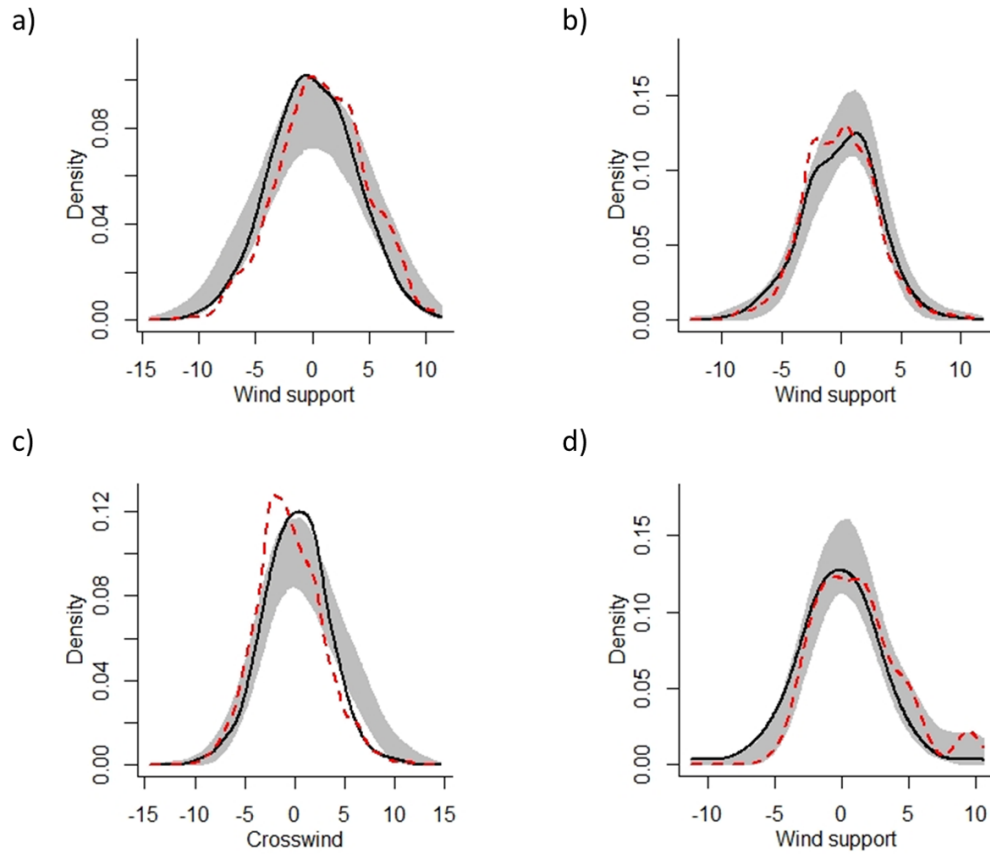


Figure S4.5. Validation of SSF using UHC plots following (Fieberg et al. 2018). Only plots for predictors that significantly influenced movement decisions (Table 4.3, Table S4.2) are presented. (a) the snowy owl, (b) and (c) the rough-legged buzzard and (d) the peregrine falcon. The black line represents the distribution of the environmental variable at used locations, the grey area represents the UHC simulation envelope, and the red line represents the distribution of alternative locations in SSF.

Appendix 5

Supplementary material to Chapter 5 -

Wing tags severely impair movement in African Cape Vultures

Teja Curk, Martina Scacco, Kamran Safi, Martin Wikelski, Wolfgang Fiedler, Ryno Kemp, Kerri Wolter

Table S5.1. Age classes by tag type and group.

Tag type	Group	Age	N of ind
Legband	Captive	Adult	0
Patagial	Captive	Adult	0
Legband	Wild	Adult	2
Patagial	Wild	Adult	4
Legband	Captive	Fledgling	0
Patagial	Captive	Fledgling	0
Legband	Wild	Fledgling	3
Patagial	Wild	Fledgling	1
Legband	Captive	Juvenile	7
Patagial	Captive	Juvenile	7
Legband	Wild	Juvenile	1
Patagial	Wild	Juvenile	2
Legband	Captive	Subadult	0
Patagial	Captive	Subadult	0
Legband	Wild	Subadult	0
Patagial	Wild	Subadult	1

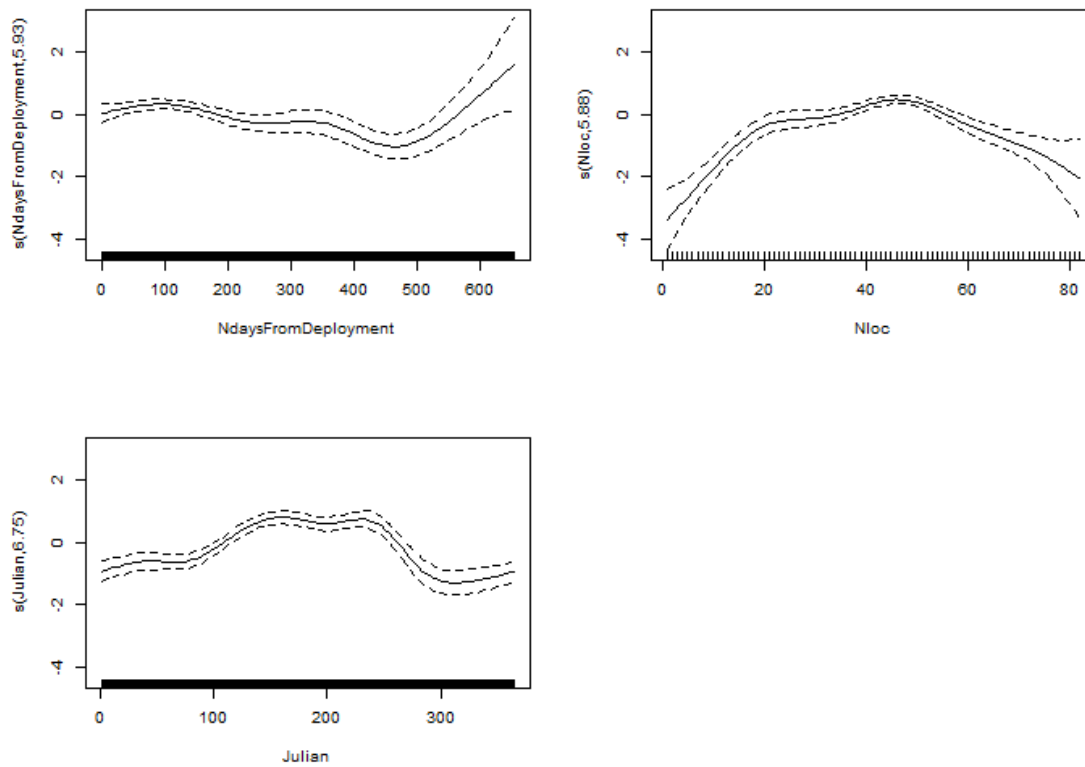


Figure S5.1. The occurrence of flight in relation to the three smooth terms included in the model: (A) number of days since deployment, (B) number of locations, and (C) Julian date.

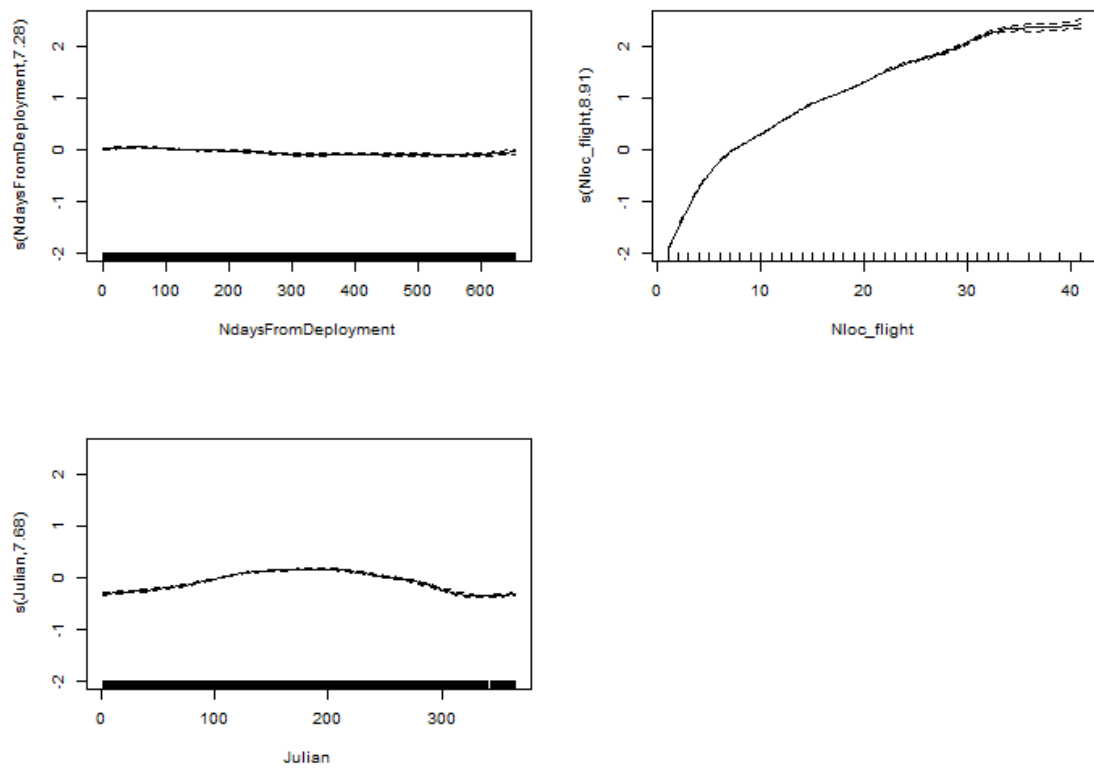


Figure S5.2. The proportion of time spend flying in relation to the three smooth terms included in the model: (A) number of days since deployment, (B) number of locations, and (C) Julian date.

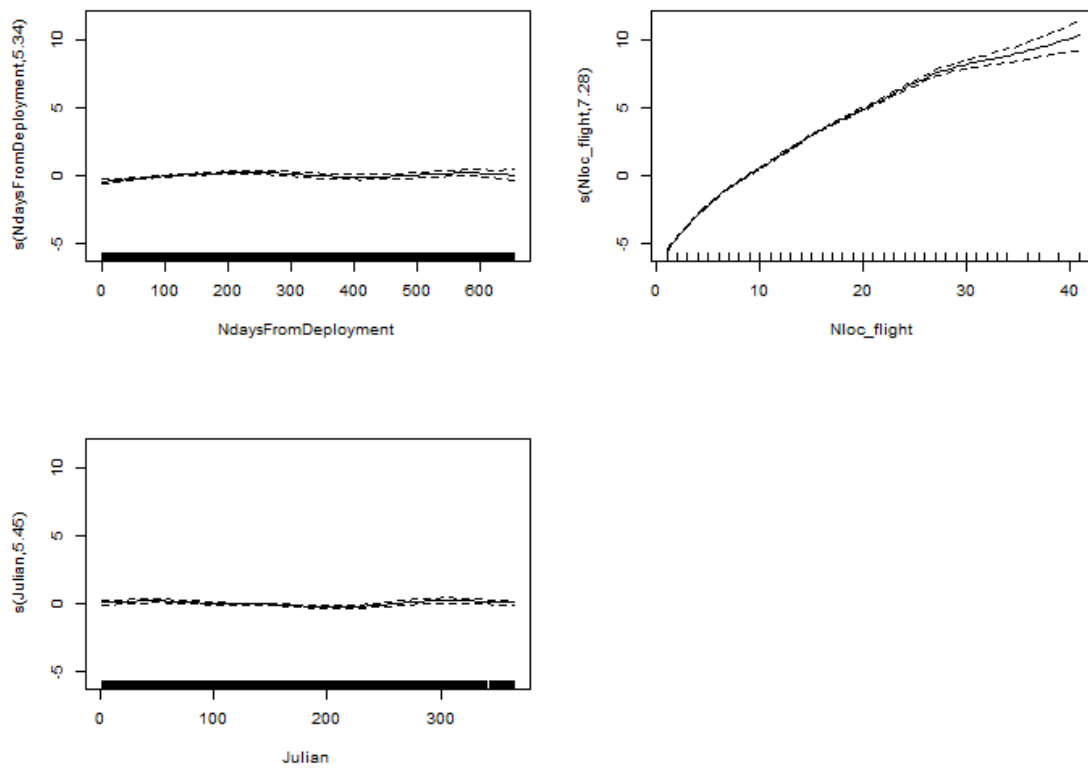


Figure S5.3. Cumulative daily distance travelled in relation to the three smooth terms included in the model: (A) number of days since deployment, (B) number of locations, and (C) Julian date.

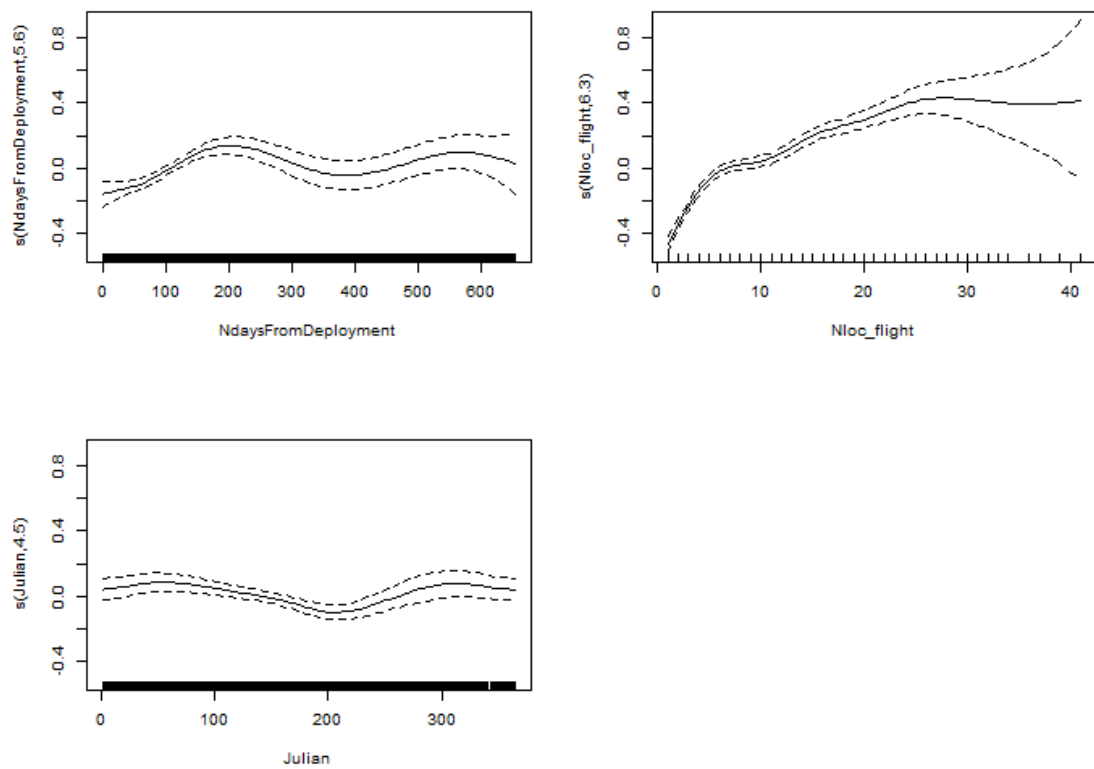


Figure S5.4. Median flight speed in relation to the three smooth terms included in the model: (A) number of days since deployment, (B) number of locations, and (C) Julian date.

References

- Alerstam, T., Hedenström, A. & Åkesson, S. (2003), 'Long-distance migration: evolution and determinants', *Oikos* **103**(2), 247–260.
- Angerbjörn, A., Tannerfeldt, M. & Lundberg, H. (2001), 'Geographical and temporal patterns of lemming population dynamics in fennoscandia', *Ecography* **24**(3), 298–308.
- Arlt, D. & Pärt, T. (2008), 'Post-breeding information gathering and breeding territory shifts in northern wheatears', *Journal of Animal Ecology* **77**(2), 211–219.
- Avgar, T., Potts, J. R., Lewis, M. A. & Boyce, M. S. (2016), 'Integrated step selection analysis: bridging the gap between resource selection and animal movement', *Methods in Ecology and Evolution* **7**(5), 619–630.
- Bannasch, R., Wilson, R. P. & Culic, B. (1994), 'Hydrodynamic Aspects of Design and Attachment of a Back-Mounted Device in Penguins', *The Journal of experimental biology* **194**(1), 83–96.
- Barbraud, C., Johnson, A. R. & Bertault, G. (2003), 'Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition', *Journal of Animal Ecology* **72**(2), 246–257.
- Barron, D. G., Brawn, J. D. & Weatherhead, P. J. (2010), 'Meta-analysis of transmitter effects on avian behaviour and ecology', *Methods in Ecology and Evolution* **1**(2), 180–187.
- Barton, K. (2019), *MuMIn: Multi-Model Inference*. R package version 1.43.15.
URL: <https://CRAN.R-project.org/package=MuMIn>
- Bastille-Rousseau, G., Gibbs, J. P., Yackulic, C. B., Frair, J. L., Cabrera, F., Rousseau, L.-P., Wikelski, M., Kümmeth, F. & Blake, S. (2017), 'Animal movement in the absence of predation: environmental drivers of movement strategies in a partial migration system', *Oikos* **126**(7), 1004–1019.
- Bastille-Rousseau, G., Potts, J. R., Yackulic, C. B., Frair, J. L., Ellington, E. H. & Blake, S. (2016), 'Flexible characterization of animal movement pattern using net squared displacement and a latent state model', *Movement ecology* **4**(1), 15.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015), 'Fitting linear mixed-effects models using lme4', *Journal of Statistical Software* **67**(1), 1–48.
- Bauer, S., Gienapp, P. & Madsen, J. (2008), 'The relevance of environmental conditions for departure decision changes en route in migrating geese', *Ecology* **89**(7), 1953–1960.
- Beardsell, A., Gauthier, G., Fortier, D., Therrien, J.-F. & Bêty, J. (2017), 'Vulnerability to geomorphological hazards of an arctic cliff-nesting raptor, the rough-legged hawk', *Arctic Science* **3**(2), 203–219.

- Beardsell, A., Gauthier, G., Therrien, J.-F. & Bêty, J. (2016), 'Nest site characteristics, patterns of nest reuse, and reproductive output in an arctic-nesting raptor, the rough-legged hawk', *Auk* **133**(4), 718–732.
- Bechard, M. J. & Swem, T. R. (2002), 'Rough-legged hawk *Buteo lagopus*', *Birds of North America* <https://birdsna.org/Species-Account/bna/species/rolhaw/introduction/>.
- Béchet, A., Giroux, J.-F., Gauthier, G., Nichols, J. D. & Hines, J. E. (2003), 'Spring hunting changes the regional movements of migrating greater snow geese', *Journal of applied ecology* **40**(3), 553–564.
- Berthold, P. (2001), *Bird migration: a general survey*, Oxford University Press.
- Bêty, J., Gauthier, G. & Giroux, J.-F. (2003), 'Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size', *The American Naturalist* **162**(1), 110–121.
- Bêty, J., Giroux, J.-F. & Gauthier, G. (2004), 'Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*)', *Behavioral Ecology and Sociobiology* **57**(1), 1–8.
- Bhatt, U. S., Walker, D. A., Raynolds, M. K., Comiso, J. C., Epstein, H. E., Jia, G., Gens, R., Pinzon, J. E., Tucker, C. J., Tweedie, C. E. et al. (2010), 'Circumpolar Arctic tundra vegetation change is linked to sea ice decline', *Earth Interact.* **14**(8), 1–20.
- Bildstein, K. L. (2006), *Migrating raptors of the world: their ecology & conservation*, Cornell University Press.
- Bilodeau, F., Gauthier, G. & Berteaux, D. (2013), 'Effect of snow cover on the vulnerability of lemmings to mammalian predators in the Canadian Arctic', *Journal of Mammalogy* **94**(4), 813–819.
- Bivand, R. S., Pebesma, E. & Gomez-Rubio, V. (2013), *Applied spatial data analysis with R, Second edition*, Springer, NY.
URL: <https://asdar-book.org/>
- Blake, S., Yackulic, C. B., Cabrera, F., Tapia, W., Gibbs, J. P., Kümmeth, F. & Wikelski, M. (2013), 'Vegetation dynamics drive segregation by body size in galapagos tortoises migrating across altitudinal gradients', *Journal of Animal Ecology* **82**(2), 310–321.
- Bloom, P., Clark, W. & Kidd, J. (2007), 'Capture techniques. 193–219', *DM Bird and KL Bildstein.[E ds.]. Raptor research and management techniques. Hancock House Publishers. Blaine, WA USA*.
- Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C. & Bearhop, S. (2018), 'A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data', *Methods in Ecology and Evolution* **9**(4), 946–955.
- Both, C., Bouwhuis, S., Lessells, C. & Visser, M. E. (2006), 'Climate change and population declines in a long-distance migratory bird', *Nature* **441**(7089), 81–83.

- Both, C., Van Turnhout, C. A., Bijlsma, R. G., Siepel, H., Van Strien, A. J. & Foppen, R. P. (2009), 'Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats', *Proceedings of the Royal Society B: Biological Sciences* **277**(1685), 1259–1266.
- Botha, A. (2007), 'A review of colour-marking techniques used on vultures in southern Africa', *Vulture News* **56**, 52–63.
URL: <http://www.ajol.info/index.php/vulnew/article/download/37662/6978>
- Bowlin, M. S., Henningsson, P., Muijres, F. T., Vleugels, R. H. E., Liechti, F. & Hedenström, A. (2010), 'The effects of geolocator drag and weight on the flight ranges of small migrants', *Methods in Ecology and Evolution* **1**(4), 398–402.
- Bradley, M., Johnstone, R., Court, G. & Duncan, T. (1997), 'Influence of weather on breeding success of peregrine falcons in the arctic', *The Auk* pp. 786–791.
- Bradley, M. & Oliphant, L. W. (1991), 'The diet of peregrine falcons in rankin inlet, northwest territories: an unusually high proportion of mammalian prey', *Condor* **93**(1), 193–197.
- Brua, R. B. (1998), 'Negative effects of patagial tags on Ruddy Ducks', *Journal of Field Ornithology* **69**(4), 530–535.
- Bruderer, B. & Boldt, A. (2001), 'Flight characteristics of birds: I. radar measurements of speeds', *Ibis* **143**(2), 178–204.
- Buchan, C., Gilroy, J. J., Catry, I. & Franco, A. M. (2020), 'Fitness consequences of different migratory strategies in partially migratory populations: A multi-taxa meta-analysis', *Journal of Animal Ecology* **89**(3), 678–690.
- Buechley, E. R. & Şekercioğlu, Ç. H. (2016), 'The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions', *Biological Conservation* **198**, 220–228.
URL: <https://doi.org/10.1016/j.biocon.2016.04.001>
- Bull, E. L. & Duncan, J. R. (1993), *Great gray owl: Strix nebulosa*, American Ornithologists' Union.
- Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J. & Ericsson, G. (2011), 'A model-driven approach to quantify migration patterns: individual, regional and yearly differences', *Journal of Animal Ecology* **80**(2), 466–476.
- Burnham, K. P. & Anderson, D. R. (2002), *Model Selection and Multimodel Inference: A practical information-theoretic approach*, 2nd ed. Springer New York.
- Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A. M., Morellet, N., Kjellander, P., Linnell, J. D., Mysterud, A., Neteler, M. et al. (2011), 'Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors', *Oikos* **120**(12), 1790–1802.
- Calabrese, J. M., Fleming, C. H. & Gurarie, E. (2016), 'ctmm: An r package for analyzing animal relocation data as a continuous-time stochastic process', *Methods in Ecology and Evolution* **7**(9), 1124–1132.

- Calenge, C. (2006a), 'The package adehabitat for the r software: tool for the analysis of space and habitat use by animals', *Ecological Modelling* **197**, 1035.
- Calenge, C. (2006b), 'The package "adehabitat" for the r software: a tool for the analysis of space and habitat use by animals', *Ecological Modelling* **197**(3-4), 516–519.
- Calvo, B. & Furness, R. W. (1992), 'A review of the use and the effects of marks and devices on birds', *Ring and Migration* **13**(3), 129–158.
- Chang, A. M. & Wiebe, K. L. (2016), 'Body condition in snowy owls wintering on the prairies is greater in females and older individuals and may contribute to sex-biased mortality', *The Auk: Ornithological Advances* **133**(4), 738–746.
- Chapman, B. B., Brönmark, C., Nilsson, J.-Å. & Hansson, L.-A. (2011), 'The ecology and evolution of partial migration', *Oikos* **120**(12), 1764–1775.
- Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. & Sheldon, B. C. (2008), 'Adaptive phenotypic plasticity in response to climate change in a wild bird population', *Science* **320**(5877), 800–803.
- Chitty, H. (1950), 'Canadian arctic wild life enquiry, 1943-49: with a summary of results since 1933', *The Journal of Animal Ecology* pp. 180–193.
- Comiso, J. C. & Hall, D. K. (2014), 'Climate trends in the Arctic as observed from space', *Wiley Interdisciplinary Reviews Climate Change* **5**(3), 389–409.
- Cooper, N. W., Sherry, T. W. & Marra, P. P. (2015), 'Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird', *Ecology* **96**(7), 1933–1942.
- Cotton, P. A. (2003), 'Avian migration phenology and global climate change', *Proceedings of the National Academy of Sciences of the United States of America* **100**(21), 12219–12222.
- Cox, G. W. (1985), 'The evolution of avian migration systems between temperate and tropical regions of the new world', *The American Naturalist* **126**(4), 451–474.
- Cramp, S. & Simmons, K. (1980), *Vol. II: Hawks to bustards*, Oxford University Press.
- Curk, T., Pokrovsky, I., Lecomte, N., Aarvak, T., Brinker, D. F., Burnham, K., Dietz, A., Dixon, A., Franke, A., Gauthier, G. et al. (2020), 'Arctic avian predators synchronise their spring migration with the northern progression of snowmelt', *Scientific reports* **10**(1), 1–11.
- Dietz, A. J., Kuenzer, C. & Dech, S. (2015), 'Global snowpack: A new set of snow cover parameters for studying status and dynamics of the planetary snow cover extent', *Remote Sensing Letters* **6**(11), 844–853.
- Dittmann, T., Zinsmeister, D. & Becker, P. H. (2005), 'Dispersal decisions: common terns, sterna hirundo, choose between colonies during prospecting', *Animal behaviour* **70**(1), 13–20.
- Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S. C., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes, D. & Wikelski, M. (2013), 'The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data', *Movement Ecology* **1**(1), 3.

- Doligez, B., Pärt, T. & Danchin, E. (2004), 'Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection?', *Animal Behaviour* **67**(3), 457–466.
- Domine, F., Gauthier, G., Vionnet, V., Fauteux, D., Dumont, M. & Barrere, M. (2018), 'Snow physical properties may be a significant determinant of lemming population dynamics in the high Arctic', *Arctic Science* **4**(4), 813–826.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J. et al. (2013), 'Collinearity: a review of methods to deal with it and a simulation study evaluating their performance', *Ecography* **36**(1), 27–46.
- Douglas, D. C., Weinzierl, R., C. Davidson, S., Kays, R., Wikelski, M. & Bohrer, G. (2012), 'Moderating Argos location errors in animal tracking data', *Methods in Ecology and Evolution* **3**(6), 999–1007.
- Duchesne, D., Gauthier, G. & Berteaux, D. (2011), 'Habitat selection, reproduction and predation of wintering lemmings in the Arctic', *Oecologia* **167**(4), 967–980.
- Duncan, J. R. & Duncan, P. A. (1998), *Northern hawk owl*, Birds of North America, Incorporated.
- Ehrich, D., Schmidt, N. M., Gauthier, G., Alisauskas, R., Angerbjörn, A., Clark, K., Ecke, F., Eide, N. E., Framstad, E., Frandsen, J. et al. (2020), 'Documenting lemming population change in the arctic: Can we detect trends?', *Ambio* **49**(3), 786–800.
- Ehrich, D., Tarroux, A., Stien, J., Lecomte, N., Killengreen, S., Berteaux, D. & Yoccoz, N. G. (2011), 'Stable isotope analysis: modelling lipid normalization for muscle and eggs from arctic mammals and birds', *Methods in Ecology and Evolution* **2**(1), 66–76.
- Fauchald, P. & Tveraa, T. (2003), 'Using first-passage time in the analysis of area-restricted search and habitat selection', *Ecology* **84**(2), 282–288.
- Fauteux, D., Gauthier, G. & Berteaux, D. (2015), 'Seasonal demography of a cyclic lemming population in the Canadian Arctic', *Journal of Animal Ecology* **84**(5), 1412–1422.
- Ferguson-Lees, J. & Christie, D. A. (2001), *Raptors of the world*, A&C Black.
- Fieberg, J. R., Forester, J. D., Street, G. M., Johnson, D. H., ArchMiller, A. A. & Matthiopoulos, J. (2018), 'Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models', *Ecography* **41**(5), 737–752.
- Fleming, C. H. & Calabrese, J. M. (2019), 'ctmm: Continuous-Time Movement Modeling'.
URL: <https://cran.r-project.org/package=ctmm>
- Forester, J. D., Im, H. K. & Rathouz, P. J. (2009), 'Accounting for animal movement in estimation of resource selection functions: sampling and data analysis', *Ecology* **90**(12), 3554–3565.
- Forstmeier, W. (2002), 'Benefits of early arrival at breeding grounds vary between males', *Journal of Animal Ecology* **71**(1), 1–9.

- Forstmeier, W. & Schielzeth, H. (2011), 'Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse', *Behavioral Ecology and Sociobiology* **65**(1), 47–55.
- Freitas, C. (2010), 'Package "argosfilter"'.
URL: <https://CRAN.R-project.org/package=argosfilter>
- Freitas, C., Lydersen, C., Fedak, M. A. & Kovacs, K. M. (2008), 'A simple new algorithm to filter marine mammal argos locations', *Marine Mammal Science* **24**(2), 315–325.
- Fuller, M. R., Seegar, W. S. & Schueck, L. S. (1998), 'Routes and travel rates of migrating peregrine falcons *Falco peregrinus* and swainson's hawks *Buteo swainsoni* in the western hemisphere', *Journal of Avian Biology* **29**, 433–440.
- Gessaman, J. A. & Nagy, K. A. (1988), 'Transmitter Loads Affect the Flight Speed and Metabolism of Homing Pigeons', *The Condor* **90**(3), 662.
- Gilg, O., Hanski, I. & Sittler, B. (2003), 'Cyclic dynamics in a simple vertebrate predator-prey community', *Science* **302**(5646), 866–868.
- Gilg, O., Sittler, B., Sabard, B., Hurstel, A., Sané, R., Delattre, P. & Hanski, I. (2006), 'Functional and numerical responses of four lemming predators in high arctic greenland', *Oikos* **113**(2), 193–216.
- Gillis, E. A., Green, D. J., Middleton, H. A. & Morrissey, C. A. (2008), 'Life history correlates of alternative migratory strategies in american dippers', *Ecology* **89**(6), 1687–1695.
- Graves, G. R., Newsome, S. D., Willard, D. E., Grosshuesch, D. A., Wurzel, W. W. & Fogel, M. L. (2012), 'Nutritional stress and body condition in the great gray owl (*Strix nebulosa*) during winter irruptive migrations', *Canadian Journal of Zoology* **90**(7), 787–797.
- Grayson, K. L., Bailey, L. L. & Wilbur, H. M. (2011), 'Life history benefits of residency in a partially migrating pond-breeding amphibian', *Ecology* **92**(6), 1236–1246.
- Greenwood, P. J. & Harvey, P. H. (1982), 'The natal and breeding dispersal of birds', *Annual review of ecology and systematics* **13**, 1–21.
- Gu, Z., Pan, S., Lin, Z., Hu, L., Dai, X., Chang, J., Xue, Y., Su, H., Long, J., Sun, M. et al. (2021), 'Climate-driven flyway changes and memory-based long-distance migration', *Nature* pp. 1–6.
- Haman, J. & Avery, M. (2020), *ciTools: Confidence or Prediction Intervals, Quantiles, and Probabilities for Statistical Models*. R package version 0.6.1.
URL: <https://CRAN.R-project.org/package=ciTools>
- Hanssen-Bauer, I., Førland, E. J., Haugen, J. E. & Tveito, O. E. (2003), 'Temperature and precipitation scenarios for norway: comparison of results from dynamical and empirical downscaling', *Climate Research* **25**(1), 15–27.
- Harel, R., Duriez, O., Spiegel, O., Fluhr, J., Horvitz, N., Getz, W. M., Bouten, W., Sarrazin, F., Hatzofe, O. & Nathan, R. (2016), 'Decision-making by a soaring bird: time, energy and risk considerations at different spatio-temporal scales', *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**(1704), 20150397.

- Hijmans, R. J. (2019a), *geosphere: Spherical Trigonometry*. R package version 1.5-10.
URL: <https://CRAN.R-project.org/package=geosphere>
- Hijmans, R. J. (2019b), *raster: Geographic Data Analysis and Modeling*. R package version 2.9-5.
URL: <https://CRAN.R-project.org/package=raster>
- Hirschauer, M. T., Wolter, K. & Forbes, N. A. (2019), 'A review of vulture wing anatomy and safe propatagial tag application methods, with case studies of injured vultures', *Journal of Wildlife Rehabilitation* **39**(3), 7–13.
- Hochachka, W. M., Wells, J. V., Rosenberg, K. V., Tessaglia-Hymes, D. L. & Dhondt, A. A. (1999), 'Irruptive migration of common redpolls', *The Condor* **101**(2), 195–204.
- Holt, D., Larson, M. D., Smith, N., Evans, D. & Parmelee, D. F. (2015a), 'Snowy owl *Bubo scandiacus*', *Birds of North America* <http://bna.birds.cornell.edu/bna/species/010>.
- Holt, D., Larson, M., Smith, N., Evans, D. & Parmelee, D. (2015b), *The Snowy Owl (Bubo scandiacus)*, In *The birds of North America*. Edited by A. Poole. Cornell Lab of Ornithology, Ithaca, N.Y.
- Ims, R. A., Henden, J.-A. & Killengreen, S. T. (2008), 'Collapsing population cycles', *Trends in Ecology and Evolution* **23**(2), 79–86.
- Johnson, A., Milne, B. & Wiens, J. (1992), 'Diffusion in fractal landscapes: simulations and experimental studies of tenebrionid beetle movements', *Ecology* **73**(6), 1968–1983.
- Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J. O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L. et al. (2006), 'Rapid advance of spring arrival dates in long-distance migratory birds', *Science* **312**(5782), 1959–1961.
- Josephson, B. (1980), 'Aging and sexing snowy owls', *Journal of Field Ornithology* pp. 149–160.
- Kane, A., Wolter, K., Neser, W., Kotze, A., Naidoo, V. & Monadjem, A. (2016), 'Home range and habitat selection of cape vultures gyps coprotheres in relation to supplementary feeding', *Bird Study* **63**(3), 387–394.
- Kattelman, R. (1991), 'Peak flows from snowmelt runoff in the Sierra Nevada, USA', *Snow, Hydrology and Forests in High Alpine Areas (Proceedings of the Vienna Symposium)* **205**, 203–211.
- Kausrud, K. L., Myserud, A., Steen, H., Vik, J. O., Østbye, E., Cazelles, B., Framstad, E., Eikeset, A. M., Myserud, I., Solhøy, T. et al. (2008), 'Linking climate change to lemming cycles', *Nature* **456**(7218), 93.
- Kay, W. P., Naumann, D. S., Bowen, H. J., Withers, S. J., Evans, B. J., Wilson, R. P., Stringell, T. B., Bull, J. C., Hopkins, P. W. & Börger, L. (2019), 'Minimizing the impact of biologging devices: using computational fluid dynamics for optimizing tag design and positioning', *Methods in Ecology and Evolution* **10**(8), 1222–1233.
- Kays, R., Crofoot, M. C., Jetz, W. & Wikelski, M. (2015a), 'Terrestrial animal tracking as an eye on life and planet', *Science* **348**(6240).

- Kays, R., Crofoot, M. C., Jetz, W. & Wikelski, M. (2015b), 'Terrestrial animal tracking as an eye on life and planet', *Science* **348**(6240).
- Kenward, R. E. (2002), 'A manual for wildlife radio tagging, 2nd edition', *Animal Conservation* **5**(3), 259–260.
- Kerlinger, P. & Lein, M. R. (1988), 'Population ecology of snowy owls during winter on the great plains of north america', *The Condor* **90**(4), 866–874.
- Kerlinger, P., Lein, M. R. & Sevick, B. J. (1985), 'Distribution and population fluctuations of wintering snowy owls (*nyctea scandiaca*) in north america', *Canadian Journal of Zoology* **63**(8), 1829–1834.
- Killick, R. & Eckley, I. (2014), 'Changepoint: an r package for changepoint analysis', *Journal of Statistical Software* **58**(3), 1–19.
- Klaassen, M., Beekman, J. H., Kontiokorpi, J., Mulder, R. J. & Nolet, B. A. (2004), 'Migrating swans profit from favourable changes in wind conditions at low altitude', *Journal of Ornithology* **145**(2), 142–151.
- Klaassen, R. H., Hake, M., Strandberg, R. & Alerstam, T. (2010), 'Geographical and temporal flexibility in the response to crosswinds by migrating raptors', *Proceedings of the Royal Society B: Biological Sciences* **278**(1710), 1339–1346.
- Koenig, W. D. & Knops, J. M. (2001), 'Seed-crop size and eruptions of north american boreal seed-eating birds', *Journal of Animal Ecology* **70**(4), 609–620.
- Kokko, H. (1999), 'Competition for early arrival in migratory birds', *Journal of Animal Ecology* **68**(5), 940–950.
- Kokko, H., Harris, M. P. & Wanless, S. (2004), 'Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *uria aalge*', *Journal of Animal Ecology* **73**(2), 367–376.
- Korner-Nievergelt, F., Baader, E., Fischer, L., Schaffner, W., Korner-Nievergelt, P. & Kestenholz, M. (2008), 'Do birds during irruption years differ from birds during "normal" years?', *Vogelwarte* **46**, 207–216.
- Kranstauber, B., Kays, R., LaPoint, S. D., Wikelski, M. & Safi, K. (2012), 'A dynamic brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement', *Journal of Animal Ecology* **81**(4), 738–746.
- Kranstauber, B., Smolla, M. & Scharf, A. (2013), 'Move: visualizing and analyzing animal track data', *R package version* **1**(360), r365.
- Kranstauber, B., Smolla, M. & Scharf, A. K. (2017), 'move: Visualizing and Analyzing Animal Track Data'.
URL: <https://cran.r-project.org/package=move>
- Kranstauber, B., Smolla, M. & Scharf, A. K. (2019), *move: Visualizing and Analyzing Animal Track Data*. R package version 3.2.2.
URL: <https://CRAN.R-project.org/package=move>

- Krebs, C. J., Kenney, A. J., Gilbert, S., Danell, K., Angerbjörn, A., Erlinge, S., Bromley, R. G., Shank, C. & Carriere, S. (2002), 'Synchrony in lemming and vole populations in the canadian arctic', *Canadian Journal of Zoology* **80**(8), 1323–1333.
- Krebs, C. J., Reid, D., Kenney, A. J. & Gilbert, S. (2011), 'Fluctuations in lemming populations in north yukon, canada, 2007–2010', *Canadian Journal of Zoology* **89**(4), 297–306.
- Krüger, S., Reid, T. & Amar, A. (2014), 'Differential range use between age classes of Southern African bearded vultures *Gypaetus barbatus*', *PLoS ONE* **9**(12), e114920.
- Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. (2017), 'lmerTest package: Tests in linear mixed effects models', *Journal of Statistical Software* **82**(13), 1–26.
- Labocha, M. K. & Hayes, J. P. (2012), 'Morphometric indices of body condition in birds: a review', *Journal of Ornithology* **153**(1), 1–22.
- Lack, D. et al. (1954), 'The natural regulation of animal numbers.', *The Natural Regulation of Animal Numbers*. .
- Lamarre, V., Franke, A., Love, O. P., Legagneux, P. & Bêty, J. (2017), 'Linking pre-laying energy allocation and timing of breeding in a migratory arctic raptor', *Oecologia* **183**(3), 653–666.
- Larson, D. L. & Bock, C. E. (1986), 'Eruptions of some north american boreal seed-eating birds, 1901–1980', *Ibis* **128**(1), 137–140.
- Le Corre, M., Dussault, C. & Côté, S. D. (2014), 'Detecting changes in the annual movements of terrestrial migratory species: using the first-passage time to document the spring migration of caribou', *Movement Ecology* **2**(1), 19.
- Liechti, F. (2006), 'Birds: blowin' by the wind?', *Journal of Ornithology* **147**(2), 202–211.
- Loe, L., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Langvatn, R., Klein, F., Calenge, C., Ergon, T., Pettorelli, N. & Stenseth, N. (2005), 'Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in norway and france', *Journal of Animal Ecology* **74**(4), 579–588.
- Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F., Nyegaard, H. & Cottaar, F. (2007), 'Effects of snow cover on the timing and success of reproduction in high-arctic pink-footed geese *Anser brachyrhynchus*', *Polar Biology* **30**(11), 1363–1372.
- Mandel, J., Bildstein, K., Bohrer, G. & Winkler, D. (2008), 'Movement ecology of migration in turkey vultures', *Proceedings of the National Academy of Sciences of the United States of America* **105**(49), 19102–19107.
- Mazerolle, M. J. et al. (2016), *AICcmodavg: Model selection and multimodel inference based on (Q) AIC (c)*. R package version 2.3-1.
URL: <https://cran.r-project.org/package=AICcmodavg>
- McGrady, M. J., Maechtle, T. L., Vargas, J. J., Seegar, W. S. & Porras Peña, M. C. (2002), 'Migration and ranging of peregrine falcons wintering on the Gulf of Mexico coast, Tamaulipas, Mexico', *Condor* **104**(1), 39–48.

- McNamara, J. M., Welham, R. K. & Houston, A. I. (1998), 'The timing of migration within the context of an annual routine', *Journal of Avian Biology* pp. 416–423.
- Monsarrat, S., Benhamou, S., Sarrazin, F., Bessa-Gomes, C., Bouten, W. & Duriez, O. (2013), 'How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers?', *PloS one* **8**(1), e53077.
- Montgomery, R. A. & Roloff, G. J. (2013), Habitat selection, in S. A. Levin, ed., 'Encyclopedia of Biodiversity (Second Edition)', second edition edn, Academic Press, Waltham, pp. 59–69.
URL: <https://www.sciencedirect.com/science/article/pii/B9780123847195003841>
- Mooij, J., Kruckenberg, H., Kondratyev, A., Zaynagutdinova, E. & Zöckler, C. (2011), 'Kolguev-island of geese', *Goose bulletin* **13**, 24–33.
- Mueller, T. & Fagan, W. F. (2008), 'Search and navigation in dynamic environments—from individual behaviors to population distributions', *Oikos* **117**(5), 654–664.
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P. E. (2008), 'A movement ecology paradigm for unifying organismal movement research', *Proceedings of the National Academy of Sciences of the United States of America* **105**(49), 19052–19059.
- Navarro, J., González-Solís, J., Viscor, G. & Chastel, O. (2008), 'Ecophysiological response to an experimental increase of wing loading in a pelagic seabird', *Journal of Experimental Marine Biology and Ecology* **358**(1), 14–19.
- Newton, I. (1970), *Finches*, Collins, London.
- Newton, I. (2006), 'Advances in the study of irruptive migration', *Ardea* **94**(3), 433.
- Newton, I. (2008), 'Irruptive migrations: owls, raptors and waterfowl', *The Migration Ecology of birds*. Elsevier, London, UK pp. 563–586.
- Newton, I. (2010), *The migration ecology of birds*, Elsevier.
- Newton, I. (2012), 'Obligate and facultative migration in birds: ecological aspects', *Journal of Ornithology* **153**(1), 171–180.
- Nourani, E., Yamaguchi, N. M., Manda, A. & Higuchi, H. (2016), 'Wind conditions facilitate the seasonal water-crossing behaviour of oriental honey-buzzards *pernis ptilorhynchus* over the east china sea', *Ibis* **158**(3), 506–518.
- Ogada, D., Shaw, P., Beyers, R. L., Buij, R., Murn, C., Thiollay, J. M., Beale, C. M., Holdo, R. M., Pomeroy, D., Baker, N., Krüger, S. C., Botha, A., Virani, M. Z., Monadjem, A. & Sinclair, A. R. (2016), 'Another Continental Vulture Crisis: Africa's Vultures Collapsing toward Extinction', *Conservation Letters* **9**(2), 89–97.
- Oksanen, L. & Oksanen, T. (1992), 'Long-term microtine dynamics in north fennoscandian tundra: the vole cycle and the lemming chaos', *Ecography* **15**(2), 226–236.
- Olofsson, J., Tommervik, H. & Callaghan, T. (2012), 'Vole and lemming activity observed from space', *Nature Climate Change* **2**(12), 880–883.

- Paradis, E. & Schliep, K. (2019), 'ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R', *Bioinformatics* **35**, 526–528.
- Pebesma, E. J. & Bivand, R. S. (2005), 'Classes and methods for spatial data in R', *R News* **5**(2), 9–13.
URL: <https://CRAN.R-project.org/doc/Rnews/>
- Pennycuick, C., Fast, P. L., Ballerstädt, N. & Rattenborg, N. (2012), 'The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves after migration', *Journal of Ornithology* **153**(3), 633–644.
- Pennycuick, C. J. (2008), *Modelling the flying bird*, Elsevier.
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jędrzejewska, B., Lima, M. & Kausrud, K. (2011), 'The normalized difference vegetation index (ndvi): unforeseen successes in animal ecology', *Climate Research* **46**(1), 15–27.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2021), *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-152.
URL: <https://CRAN.R-project.org/package=nlme>
- Poessel, S. A., Brandt, J., Miller, T. A. & Katzner, T. E. (2018), 'Meteorological and environmental variables affect flight behaviour and decision-making of an obligate soaring bird, the california condor *gymnogyps californianus*', *Ibis* **160**(1), 36–53.
- Pokrovsky, I., Ehrich, D., Ims, R. A., Kondratyev, A. V., Kruckenberg, H., Kulikova, O., Mihnevich, J., Pokrovskaya, L. & Shienok, A. (2015), 'Rough-legged buzzards, arctic foxes and red foxes in a tundra ecosystem without rodents', *PLoS One* **10**(2), e0118740.
- Pokrovsky, I., Ehrich, D., Ims, R. A., Kulikova, O., Lecomte, N. & Yoccoz, N. (2012), 'Assessing the causes of breeding failure among the rough-legged buzzard (*buteo lagopus*) during the nestling period', *Polar Research* **31**(1), 17294.
- Pokrovsky, I., Ehrich, D., Ims, R. A., Kulikova, O., Lecomte, N. & Yoccoz, N. G. (2014), 'Diet, nesting density, and breeding success of rough-legged buzzards (*Buteo lagopus*) on the Nenetsky Ridge, Arctic Russia', *Polar Biology* **37**(4), 447–457.
- Portugal, S. J. & White, C. R. (2018), 'Miniaturization of biologgers is not alleviating the 5% rule', *Methods in Ecology and Evolution* **9**(7), 1662–1666.
- Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., Hebblewhite, M., Kerby, J., Kutz, S. J., Stirling, I. & Walker, D. A. (2013), 'Ecological consequences of sea-ice decline', *Science* **341**(6145), 519–524.
- Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., Fox, A. D., Gilg, O., Hik, D. S., Høye, T. T. et al. (2009), 'Ecological dynamics across the Arctic associated with recent climate change', *Science* **325**(5946), 1355–1358.
- Potapov, E. & Sale, R. (2013), *The snowy owl*, A&C Black.
- Potts, J. R., Bastille-Rousseau, G., Murray, D. L., Schaefer, J. A. & Lewis, M. A. (2014), 'Predicting local and non-local effects of resources on animal space use using a mechanistic step selection model', *Methods in Ecology and Evolution* **5**(3), 253–262.

- Potts, J. R., Mokross, K., Stouffer, P. C. & Lewis, M. A. (2014), 'Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds', *Ecology and Evolution* **4**(24), 4578–4588.
- Powell, L. A., Lang, J. D., Krementz, D. G. & Conroy, M. J. (1998), 'Effects of radio transmitters on migrating Wood Thrushes', *Journal of Field Ornithology* **69**(2), 306–315.
- Pravosudov, V. V., Kitaysky, A. S. & Omanska, A. (2006), 'The relationship between migratory behaviour, memory and the hippocampus: an intraspecific comparison', *Proceedings of the Royal Society B: Biological Sciences* **273**(1601), 2641–2649.
- Predavec, M., Krebs, C. J., Danell, K. & Hyndman, R. (2001), 'Cycles and synchrony in the collared lemming (*Dicrostonyx groenlandicus*) in arctic north america', *Oecologia* **126**(2), 216–224.
- R Core Team (2019), 'R: A Language and Environment for Statistical Computing'.
URL: <https://www.r-project.org/>
- Ramos, D. L., Pizo, M. A., Ribeiro, M. C., Cruz, R. S., Morales, J. M. & Ovaskainen, O. (2020), 'Forest and connectivity loss drive changes in movement behavior of bird species', *Ecography* **43**(8), 1203–1214.
- Reading, R. P., Azua, J., Garrett, T., Kenny, D., Lee, H., Paek, W. K., Reece, N., Tsolmonjav, P., Willis, M. J. & Wingard, G. (2020), 'Differential movement of adult and juvenile Cinereous Vultures (*Aegypius monachus*) in Northeast Asia', *Journal of Asia-Pacific Biodiversity* **13**(2), 156–161.
- Reading, R. P., Maude, G., Hancock, P., Kenny, D. & Garbett, R. (2015), 'Comparing different types of patagial tags for use on vultures', *Vulture News* **67**(2), 33.
- Reid, D. G., Bilodeau, F., Krebs, C. J., Gauthier, G., Kenney, A. J., Gilbert, B. S., Leung, M. C.-Y., Duchesne, D. & Hofer, E. (2012), 'Lemming winter habitat choice: a snow-fencing experiment', *Oecologia* **168**(4), 935–946.
- Riotte-Lambert, L. & Matthiopoulos, J. (2020), 'Environmental predictability as a cause and consequence of animal movement', *Trends in ecology & evolution* **35**(2), 163–174.
- Robillard, A., Gauthier, G., Therrien, J.-F. & Bêty, J. (2018), 'Wintering space use and site fidelity in a nomadic species, the snowy owl', *Journal of Avian Biology* **49**(5), jav–01707.
- Robillard, A., Gauthier, G., Therrien, J.-F., Fitzgerald, G., Provencher, J. F. & Bêty, J. (2017), 'Variability in stable isotopes of snowy owl feathers and contribution of marine resources to their winter diet', *Journal of Avian Biology* **48**(6), 759–769.
- Robillard, A., Therrien, J., Gauthier, G., Clark, K. & Bêty, J. (2016), 'Pulsed resources at tundra breeding sites affect winter irruptions at temperate latitudes of a top predator, the snowy owl', *Oecologia* **181**(2), 423–433.
- Robinson, B. G., Franke, A. & Derocher, A. E. (2014), 'The influence of weather and lemmings on spatiotemporal variation in the abundance of multiple avian guilds in the Arctic', *PLoS One* **9**(7), e101495.

- Ruxton, G. D. & Houston, D. C. (2004), 'Obligate vertebrate scavengers must be large soaring fliers', *Journal of Theoretical Biology* **228**(3), 431–436.
- Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., Cruz, S., Proaño, C., Takekawa, J. Y., Newman, S. H. et al. (2013), 'Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight', *Movement Ecology* **1**(1), 4.
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K. et al. (2010), 'Climate warming, ecological mismatch at arrival and population decline in migratory birds', *Proceedings of the Royal Society B: Biological Sciences* **278**(1707), 835–842.
- Seidensticker, M. T., Holt, D. W., Detienne, J., Talbot, S. & Gray, K. (2011), 'Sexing young snowy owls', *Journal of Raptor Research* **45**(4), 281–289.
- Serreze, M. C. & Barry, R. G. (2011), 'Processes and impacts of Arctic amplification: A research synthesis', *Global and Planetary Change* **77**(1-2), 85–96.
- Shariatinajafabadi, M., Wang, T., Skidmore, A. K., Toxopeus, A. G., Kölzsch, A., Nolet, B. A., Exo, K.-M., Griffin, L., Stahl, J. & Cabot, D. (2014), 'Migratory herbivorous waterfowl track satellite-derived green wave index', *PLoS One* **9**(9), e108331.
- Shelford, V. (1945), 'The relation of snowy owl migration to the abundance of the collared lemming', *The Auk* **62**(4), 592–596.
- Si, Y., Xin, Q., De Boer, W. F., Gong, P., Ydenberg, R. C. & Prins, H. H. (2015), 'Do arctic breeding geese track or overtake a green wave during spring migration?', *Scientific Reports* **5**, 8749.
- Signer, J., Fieberg, J. & Avgar, T. (2019), 'Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses', *Ecology and Evolution* **9**(2), 880–890.
- Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N. & Ericsson, G. (2012), 'From migration to nomadism: movement variability in a northern ungulate across its latitudinal range', *Ecological Applications* **22**(7), 2007–2020.
- Smith, N. (1997), 'Observations of wintering snowy owls (*nyctea scandiaca*) at logan airport, east boston, massachusetts from 1981-1997. in: Duncan, james r.; johnson, david h.; nicholls, thomas h., eds. biology and conservation of owls of the northern hemisphere: 2nd international symposium. gen. tech. rep. nc-190. st. paul, mn: U.s. dept. of agriculture, forest service, north central forest experiment station. 591-596.'
- Solheim, R. (2012), 'Wing feather moult and age determination of snowy owls *bubo scandiacus*', *Ornis Norvegica* **35**, 48–67.
- Sonerud, G. (1997), 'Hawk owls in fennoscandia: population fluctuations, effects of modern forestry, and recommendations on improving foraging habitats', *Journal of Raptor Research* **31**(2), 167–174.

- Sonerud, G. A. (1986), 'Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia', *Ecography* **9**(1), 33–47.
- Spiess, A.-N. & Neumeyer, N. (2010), 'An evaluation of r^2 as an inadequate measure for nonlinear models in pharmacological and biochemical research: a monte carlo approach', *BMC pharmacology* **10**(1), 6.
- Stutchbury, B. J., Tarof, S. A., Done, T., Gow, E., Kramer, P. M., Tautin, J., Fox, J. W. & Afanasyev, V. (2009), 'Tracking long-distance songbird migration by using geolocators', *Science* **323**(5916), 896.
- Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. (2004), 'Large-scale spatial dynamics of vole populations in finland revealed by the breeding success of vole-eating avian predators', *Journal of Animal Ecology* **73**(1), 167–178.
- Switzer, P. V. (1993), 'Site fidelity in predictable and unpredictable habitats', *Evolutionary Ecology* **7**(6), 533–555.
- Tarroux, A., Berteaux, D. & Bêty, J. (2010), 'Northern nomads: ability for extensive movements in adult arctic foxes', *Polar Biology* **33**(8), 1021–1026.
- Tast, J., Kaikusalo, A. & Lagerström, M. (2010), 'Breeding biology of rough-legged buzzards *buteo lagopus* at kilpisjärvi, nw finnish lapland, in relation to rodent cycles', *Kilpisjärvi Notes* **22**, 1–9.
- Taylor, S. S., Leonard, M. L., Boness, D. J. & Majluf, P. (2001), 'Foraging trip duration increases for Humboldt Penguins tagged with recording devices', *Journal of Avian Biology* **32**(4), 369–372.
- Teitelbaum, C. S. & Mueller, T. (2019), 'Beyond migration: causes and consequences of nomadic animal movements', *Trends in ecology & evolution* **34**(6), 569–581.
- Therneau, T. (2015), *Mixed effects Cox models*. R package version 2.2-14.
URL: <https://CRAN.R-project.org/package=coxme>
- Therrien, J.-F., Gauthier, G., Pinaud, D. & Bêty, J. (2014), 'Irruptive movements and breeding dispersal of snowy owls: a specialized predator exploiting a pulsed resource', *Journal of Avian Biology* **45**(6), 536–544.
- Therrien, J.-F., Pinaud, D., Gauthier, G., Lecomte, N., Bildstein, K. L. & Bety, J. (2015), 'Is pre-breeding prospecting behaviour affected by snow cover in the irruptive snowy owl? A test using state-space modelling and environmental data annotated via Movebank', *Movement Ecology* **3**(1), 1.
- Thurfjell, H., Ciuti, S. & Boyce, M. S. (2014), 'Applications of step-selection functions in ecology and conservation', *Movement Ecology* **2**(1), 4.
- Tøttrup, A. P., Thorup, K., Rainio, K., Yosef, R., Lehikoinen, E. & Rahbek, C. (2008), 'Avian migrants adjust migration in response to environmental conditions en route', *Biology Letters* **4**(6), 685–688.

- Trefry, S. A., Diamond, A. W. & Jesson, L. K. (2013), 'Wing marker woes: a case study and meta-analysis of the impacts of wing and patagial tags', *Journal of Ornithology* **154**(1), 1–11.
- Vandenabeele, S. P., Grundy, E., Friswell, M. I., Grogan, A., Votier, S. C. & Wilson, R. P. (2014), 'Excess baggage for birds: Inappropriate placement of tags on gannets changes flight patterns', *PLoS ONE* **9**(3), e92657.
URL: <http://dx.plos.org/10.1371/journal.pone.0092657>
- Vandenabeele, S. P., Shepard, E. L., Grogan, A. & Wilson, R. P. (2012), 'When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints', *Marine Biology* **159**(1), 1–14.
- Vandenabeele, S. P., Wilson, R. P. & Wikelski, M. (2013), 'New tracking philosophy for birds', *Frontiers in Ecology and the Environment* **11**(1), 10–12.
- Verboom, J., Schippers, P., Cormont, A., Sterk, M., Vos, C. C. & Opdam, P. F. (2010), 'Population dynamics under increasing environmental variability: implications of climate change for ecological network design criteria', *Landscape ecology* **25**(8), 1289–1298.
- Vergara, P., I. Aguirre, J. & Fernández-Cruz, M. (2007), 'Arrival date, age and breeding success in white stork *ciconia ciconia*', *Journal of Avian Biology* **38**(5), 573–579.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002), 'Ecological responses to recent climate change', *Nature* **416**(6879), 389.
- Wanless, S., Harris, M. P. & Morris, J. A. (1989), 'Behavior of Alcids with Tail-Mounted Radio Transmitters', *Colonial Waterbirds* **12**(2), 158–163.
- Ward, M. P. (2005), 'Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information', *Oecologia* **145**(4), 650–657.
- White, C. M., Clum, N. J., Cade, T. J. & Hunt, W. G. (2002), 'Peregrine falcon *Falco peregrinus*', *Birds of North America* <https://birdsna.org/Species-Account/bna/species/perfal/introduction>.
- Williams, H. J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., Grissac, S., Demšar, U., English, H. M., Franconi, N., Gómez-Álamo, A., Griffiths, R. C., Kay, W. P., Morales, J. M., Potts, J. R., Rogerson, K. F., Rutz, C., Spelt, A., Trevail, A. M., Wilson, R. P. & Börger, L. (2020), 'Optimizing the use of biologgers for movement ecology research', *Journal of Animal Ecology* **89**(1), 186–206.
- Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E. & Yovovich, V. (2015), 'The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology', *Ecology* **96**(7), 1741–1753.
- Wilson, R. P. & Wilson, M.-p. T. J. (1989), 'Tape: A Package-Attachment Technique for Penguins', *Wildlife Society Bulletin* **17**(1), 77–79.
- Winkler, D. W., Wrege, P. H., Allen, P. E., Kast, T. L., Senesac, P., Wasson, M. F., Llambías, P. E., Ferretti, V. & Sullivan, P. J. (2004), 'Breeding dispersal and philopatry in the tree swallow', *The Condor* **106**(4), 768–776.

- Wolter, K., Naser, W. & Hirschauer, M. (2018), 'Protocols for mass capturing, handling, and fitting tracking devices and patagial (wing) tags on vultures - version 3.0'.
URL: <https://vulpro.com/wp-content/uploads/2020/02/Wolter-et-al-Protocols-for-Mass-Capture-Handling-and-Fitting-tracking-devices-on-Gyps-vultures-V3.0-Nov-20181.pdf>
- Wood, S. N. (2003), 'Thin plate regression splines', *Journal of the Royal Statistical Society. Series B: Statistical Methodology* **65**(1), 95–114.
- Yamaguchi, N. M., Hiraoka, E., Hijikata, N. & Higuchi, H. (2017), 'Migration routes of satellite-tracked Rough-legged Buzzards from Japan: the relationship between movement patterns and snow cover', *Ornithological Science* **16**(1), 33–41.
- Zuberogoitia, I., Arroyo, B., O'Donoghue, B., Zabala, J., Martínez, J. A., Martínez, J. E. & Murphy, S. G. (2012), 'Standing out from the crowd: Are patagial wing tags a potential predator attraction for harriers (*Circus* spp.)?', *Journal of Ornithology* **153**(3), 985–989.

Author contributions

Chapter 1

Winter irruptive Snowy Owls (*Bubo scandiacus*) in North America are not starving

TC, JFT, GG and NL conceived the study. TM, DZ, SW, DB, SH, NS, TM and AR trapped, aged and measured snowy owls. TC conducted the analyses and wrote the first draft of the manuscript. All co-authors commented on the manuscript and approved the final version for publication.

Chapter 2

Contrasting movement patterns are the snowy owls' response to difference in resource variability

TA, DFB, GG, KOJ, IJØ, RS, SW, KW and JFT provided the data. TC designed the study and analyzed the data under the supervision of KS and PhD committee members IP, NL, JFT and MW. TC wrote the first draft of the manuscript and all co-authors provided valuable comments on the manuscript.

Chapter 3

Arctic migratory raptor selects nesting area during the previous breeding season

IP developed the project idea. TC and IP analysed the data and wrote the manuscript. IP, OK, and MW prepared the database. KS provided valuable suggestions for data analyses. IP, OK, IF, MW, and TC conducted fieldwork. MW obtained funding. All authors took part in the preparation of the manuscript including logical interpretation and presentation of the results.

Chapter 4

Arctic avian predators synchronise their spring migration with the northern progression of snowmelt

KS, IP, NL, JFT, and MW participated in discussions and provided valuable feedback on the study design and data analyses. TC carried out the study. ADie provided snow cover data and performed interpolation of snow cover rasters to remove the effects of clouds and darkness. TC wrote the manuscript with significant input from KS, IP, NL, JFT, and MW. IP, NL, TA, DFB, KB, ADix, AF, GG, KOJ, JK, SBL, IJØ, AS, VS, RS, SW, KW, and JFT shared tracking data and provided valuable comments on the manuscript. All authors read and approved the final manuscript for publication.

Chapter 5

Wing tags severely impair movement in African Cape Vultures

KW designed the study and provided the data. TC, MS and KS analysed and interpreted the data and wrote the first draft of the manuscript. KW, RK, WF and MW provided valuable comments on the manuscript. All authors read and approved the final version of the manuscript. TC and MS contributed equally to this work and are co-first authors.

Acknowledgements

First of all, I want to thank Kami for giving me the opportunity to be part of the lab and for the guidance and support throughout the years. It has been a challenging but stimulating and exciting couple of years during which I have learned a lot and have grown not only professionally but also as a person. A big thank goes to Martin for making all this possible and for the eternal enthusiasm and encouragement. Many thanks also to the members of my PhD advisory committee: Niko, JF, Ivan, Kami and Martin. Thanks for all the support, your comments on the million versions of manuscripts and for the combination of discussing science and fun during our PAC meetings. Thanks also to the members of the examination committee: Dina, Niko and Martin for reviewing the thesis. Thanks, Anja for checking the German translation of the summary. Special thanks go to the current and previous Safi lab members: Anne, Alaa, Elham, Hannah, Kevin, Martina and Matthias. Thanks for all your help, interesting discussions during lab meetings and eating sushi on Fridays. I also want to thank current and previous members of the Dechmann lab: Dina, Camila, Javi, Jenna, Lara and Marion for joined lab meetings and countless cakes. Thanks also to Myles and Yachang and to those who were visiting the institute: Alberto, Antonella, Eneko, Erik, Ettore, Milene, Paolo, Reyes and Valentina. Thanks to Ivan and Olga for the adventures during the expedition in Kolguyev Island. A big thank goes to the former and current coordinator of the IMPRS, Mäggi and Francisca for providing help with bureaucratic matters that allowed me to go through all stages of the PhD. Thanks to all current and former IMPRS students for learning together during the IMPRS courses and at the same time all the fun during the retreats and other events. It was really nice to meet every one of you. Many thanks also to the administration personal, especially Jenn, Elke and Sabine for all (very needed) help with paperwork. Thanks also to all colleagues at the MPI who in some way or another helped me to grow as a scientist. Many thanks to my friends for all the fun we had during the last years in Konstanz. Thanks to Camilla, Hemal, Jacob, Jenna, Jessie, Lara, Martina, Stefano and Vivek for delicious food and playing music during our brunches. Thanks, Jenna and Lara for being the most dedicated beach volleyball players even when it is cold and we need to play in socks. Thanks, Baptiste for always organising squash. Thanks, Hemal for birding walks even when it is very early and nobody else would be willing to wake up. Thanks, Jessie and Jenna for always being up for swimming, amazing hikes in the Alps, sleeping on the top of the mountains and watching shooting stars. Thanks also to Matthias for crazy hiking in the snow and combining several day hikes into one. Thanks, Camilla, Jenna, Jessie and Martina for girly pajama-parties, doing hairstyles and painting nails. Thanks, Jenna for guitar, ukulele and piano evenings, visiting Christmas markets and crocheting on the train.

Thanks, Vivek for cooking Indian food so many times for me, for running a half marathon, walks in the forest, "gossip" and jokes that only kids understand. The biggest thanks go to Hugo, my partner who I am so lucky to have and who was always supporting me and went with me through the ups and downs of the PhD. Thanks to my dog Billy who was "helping" to write the thesis only by sleeping on my feet. Many thanks also to my family: mama, ata, babi, Tine, Samek and Kori. Thank you everyone for helping me to get where I am now. I dedicate this thesis to all of you.

List of publications

Curk, T.*, Scacco, M.*, Safi, K., Wikelski, M., Fiedler, W., Kemp, R. & Wolter, K. (2021). Wing tags severely impair movement in African Cape Vulture. *Animal Biotelemetry*, 9, 1-13.

Delmore, K., Van Doren, B. M., Conway, G. J., **Curk, T.**, Garrido-Garduño, T., Germain, R. R., Hasselmann, T., Hiemer, D., van der Jeugd, H. P., Justen, H., Lugo Ramos, J. S., Maggini, I., Meyer, B. S., Phillips, R. J., Remisiewicz, M., Roberts, G. C. M., Sheldon, B. C., Vogl, W. & Liedvogel, M. (2020). Individual variability and versatility in an eco-evolutionary model of avian migration. *Proceedings of the Royal Society B*, 287, 20201339.

Curk, T., Pokrovsky, I., Lecomte, N., Aarvak, T., Brinker, D. F., Burnham, K., Dietz, A., Dixon, A., Franke, A., Gauthier, G., Jacobsen, K-O., Kidd, J., Lewis, S. B., Øien, I. J., Sokolov, A., Sokolov, V., Solheim, R., Weidensaul, S., Wiebe, K., Wikelski, M., Therien, J-F. & Safi, K. (2020). Arctic avian predators synchronise their spring migration with the northern progression of snowmelt. *Scientific Reports*, 10, 1-11.

Baldan, D., **Curk, T.**, T., Hinde, C. A. & Lessells, C. M. (2019). Alternation of nest visits varies with experimentally manipulated workload in brood-provisioning great tits. *Animal Behaviour*, 156, 139-146.

Curk, T., McDonald, T., Zazelenchuk, D., Weidensaul, S., Brinker, D., Huy, S., Smith, N., Miller, T., Robillard, A., Gauthier, G. & Lecomte, N. (2018). Winter irruptive Snowy Owls (*Bubo scandiacus*) in North America are not starving. *Canadian Journal of Zoology*, 96, 553

Note that authors with a * are co-first authors.