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Tracking behavioural trajectories: early-life effects on natal dispersal patterns in golden eagles (*Aquila chrysaetos*)

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Julia Solveig Hatzl
M.Sc. University Zurich

born on 24.02.1992

accepted on the recommendation of

Prof. Dr. Loïc Pellissier
Dr. Martin Urs Grüebler
Dr. Andrea Flack

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Summary

The study of movement and behavioural differences among individuals as well as the mechanisms behind it are increasingly recognised as being crucial for ecological processes. In an individual's early life, external and internal conditions interact and shape behavioural phenotypes which can carry-over to later life stages. Although the importance of early-life for understanding later fitness-relevant behaviours is acknowledged, studies relating early behaviours to natal dispersal movement patterns in the wild are still rare. Especially in highly mobile species such as birds, the extensive space use after leaving the nest makes it difficult to collect detailed longitudinal data. In this thesis, I capitalised on technological advancements to quantify individual behavioural differences during the nestling and post-fledging period of golden eagles (*Aquila chrysaetos*) using GPS and accelerometer data. I then used these early behavioural differences to investigate carry-over effects on the timing of emigration from the parental territory and the subsequent movement and space use characteristics.

In the first chapter, I investigated the carry-over effects of the nestlings' activity phenotype throughout the post-fledging dependency period. I showed that high activity levels were associated with high nestling body condition and that active nestlings fledged earlier and were more active during the post-fledging period before emigrating at a younger age compared to their less-active peers. Thus, the early activity phenotype was consistent throughout the post-fledging period and was related to the onset of dispersal, with potential important consequences for dispersal behaviour and recruitment. In the second chapter I investigated the consequences of early post-fledging differences in feeding behaviour and flight skill development upon age at emigration. I found that frequent feeding and increased flight efficiency, characterised by the proportion of time spent soaring versus flapping, was associated with early emigration were both associated with a young emigration age, which suggests that the quality of the parental territory in terms of food and uplift availability plays a key role in shaping the maturation of young soaring birds with consequences for dispersal behaviour. In the third chapter, I focussed on the association between emigration age and post-emigration movement patterns. I found that an early emigration age was linked to reduced mobility in the time just after emigration. However, mobility of early emigrating individuals increased over the pre-reproductive years resulting in higher mobility than that of late emigrating conspecifics. The results indicate that early emigrating individuals might profit from competitive advantages over late emigrating individuals and compete earlier with breeding birds over territories. To conclude, in my fourth chapter I explored the effect of the social environment of territorial breeding birds upon habitat selection of juveniles throughout the years of natal dispersal. Transient juveniles avoided habitats in proximity to existing territory centres, and this effect was stronger during periods of encampment than during periods of exploratory movement behaviour. Consequently, transient juveniles preferred remote areas within territories during encampment and areas near territory borders during exploratory movements. These results indicate that in hight density populations of territorial species, space and thus resources available to juveniles are limited and restricted to areas of low territorial defence behaviour of breeding adults. The results of my thesis suggest that between-individual behavioural differences show cascading effects from early life to later life-history stages, thereby accumulating the associated costs and benefits over multiple life stages to affect dispersal and recruitment processes.

Zusammenfassung

Bewegungs- und Verhaltensunterschiede sowie die zugrundeliegenden Mechanismen bekommen immer mehr Gewichtung bei der Untersuchung von demographischen Prozessen. In den frühen Lebensphasen eines Individuums interagieren äussere mit inneren Bedingungen und formen Verhaltensphänotypen, die lebenslang fortbestehen und die Fitness eines Individuums beeinflussen können. Obwohl die Bedeutung der frühen Lebensphase für das Verständnis fitnessrelevanter Verhaltensweisen im späteren Leben anerkannt ist, gibt es nur wenige Studien, die frühes Verhalten mit den Bewegungsmustern während späteren Lebensabschnitten in Verbindung bringen. Speziell bei sehr mobilen Arten wie Vögeln erschwert die ausgedehnte Raumnutzung nach dem Verlassen des Nests das Sammeln von detaillierten Langzeitdaten. In dieser Arbeit nutzte ich technologische Neuheiten, um individuelle Verhaltensunterschiede während der Nestlings- und elterlichen Abhängigkeitsphase von Steinadlern (*Aquila chrysaetos*) mithilfe von GPS- und Beschleunigungsdaten zu quantifizieren. Diese frühen Verhaltensunterschiede nutzte ich, um Übertragungseffekte auf den Zeitpunkt der Abwanderung aus dem elterlichen Revier und die anschliessende Raumnutzung zu untersuchen.

Im **ersten Kapitel** untersuchte ich die Übertragungseffekte des Aktivitätsphänotyps der Nestlinge auf die Phase der eltlichen Abhängigkeit nach dem verlassen des Nests. Ich zeigte, dass hohe Aktivitätsniveaus mit einer guten Körperkondition der Nestlinge verbunden waren und dass aktive Nestlinge früher das Nest verliessen. Diese Nestlinge waren während der elterlichen Abhängigkeitsphase aktiver und verliessen das elterliche Revier früher als ihre weniger aktiven Artgenossen. Der frühe Aktivitätsphänotyp war somit während der Nestlings- sowie der elterlichen Abhängikeitsphase konsistent und stand im Zusammenhang mit den vorherrschenden Bedingungen während der frühen Entwicklung. Potenziell haben solche Aktivitätsphänotypen wichtige Konsequenzen für das Abwanderungsverhalten und die Rekrutierung in die Brutpopulation im späteren Leben. Im **zweiten Kapitel** untersuchte ich die Folgen früher Unterschiede im Fressverhalten und der Entlicklung des Flugverhaltens nach dem Ausfliegen aus dem Nest auf das Alter des Abwanderns aus dem elterlichen Revier. Ich stellte fest, dass häufiges Fressen und eine erhöhte Flugeffizienz—gekennzeichnet durch den Anteil der Zeit, die im Segelflug anstatt mit

aktivem Flügelschlag verbracht wurde—beide mit einem frühen Abwanderungszeitpunkt verbunden waren. Dies deutet darauf hin, dass die Qualität des elterlichen Territoriums in Bezug auf Nahrungsverfügbarkeit und Aufwinde eine entscheidende Rolle beim heranwachsen junger Vögel spielt. Im **dritten Kapitel** konzentrierte ich mich auf den Zusammenhang zwischen dem Emigrationsalter und den Bewegungsmustern nach der Abwanderung aus dem elterlichen Revier. Ich fand heraus, dass ein früher Abwanderungszeitpunkt mit einer reduzierten Mobilität in der Zeit unmittelbar nach der Emigration verbunden war. Allerdings nahm die Mobilität der früh abwandernden Individuen in den prä-reproduktiven Jahren zu und übertraf letztlich die Mobilität der spät abwandernden Artgenossen. Die Ergebnisse deuten darauf hin, dass früh abwandernde Individuen möglicherweise von kompetitiven Vorteilen, die sie sich im frühen Lebensabschnitt aneignen, gegenüber spät emigrierenden Individuen profitieren. Diese Vorteile könnten es ihnen ermöglihcen, früher in Leben mit Brutvögeln um Territorien zu konkurrieren und erfolgreich Territorien zu übernehmen. Abschliessend untersuchte ich im **vierten Kapitel** den Einfluss des sozialen Umfelds, das durch territoriale Brutvögel gebildet wird, auf die Habitatwahl von Jungvögeln während der Wanderjahre nach Verlassen des elterlichen Revieres. Während der Wanderjahre mieden Jungvögel Lebensräume in der Nähe bestehender Territorialzentren. Dieser Effekt war während Phasen von räumlich konzentrierten Bewegungsverhalten stärker ausgeprägt als während explorativen Phasen. Folglich bevorzugten wandernde Jungvögel abgelegene Gebiete in Randgebieten von Territorien während des räumlich konzentrierten Bewegungsverhaltens. Während explorativen Bewegungen war dieses Meiden ein wenig schwächer ausgeprägt. Diese Ergebnisse deuten darauf hin, dass in dicht besiedelten Populationen territorialer Arten der Raum und damit die den Jungvögeln zur Verfügung stehenden Ressourcen begrenzt und auf Gebiete mit geringer territorialer Verteidigung beschränkt sind. Die Ergebnisse meiner Arbeit legen nahe, dass interindividuelle Verhaltensunterschiede Kaskadeneffekte von der frühen Lebensphase bis zu späteren Lebensstadien auslösen und somit die damit verbundenen Kosten und Vorteile über mehrere Lebensphasen akkumuliert werden, die potentiell Ausbreitungs- und Rekrutierungsprozesse beeinflussen können.

1. General Introduction

Illustration: Lara Gross

> “The road goes ever on and on
> Down from the door where it began.
> Now far ahead the road has gone,
> And I must follow, if I can,
> Pursuing it with eager feet,
> Until it joins some larger way,
> Where many paths and errands meet.”
> — J.R.R. Tolkien, The Lord of the Rings

Movement Behaviour in Animals

The movement of animals is fundamental for determining not only individual fitness, but also population- and community-structures. Movement enables animals to exploit spatially and temporally variable resources (Rémy et al., 2011). On the one hand, the decision to move and the subsequent routes chosen depend on external factors, such as predation (Dickie et al., 2023), competition (Stamps, 1991), food availability (Reyna-Hurtado et al., 2018), or mating prospects (Torsekar & Thaker, 2020). On the other hand, movement is affected by internal factors such as an individual's genetic predisposition (Shaw, 2020), sex (Barbraud et al., 2003), and age (Lubitz et al., 2022.). Across increasing spatiotemporal scales, the movement trajectory of an animal can be divided up into different movement behaviours, like foraging and resting, larger-scale exploratory movements (exploration) and slow, spatially restricted movements (encampment) as well as dispersal and migration (Nathan et al., 2008). Animals need to adapt their movements to reflect their current needs and the surrounding environmental factors (Grenier-Potvin et al., 2021; Mohlenhoff et al., 2017) in order to optimise benefits and minimise costs associated with movement (Suraci et al., 2019). For instance, individuals often forage in resource rich patches, rest in areas that provide shelter (Suraci et al., 2019) and move along structures that facilitate energy-efficient movement (Dickie et al., 2017; Murgatroyd et al., 2018). Understanding the processes that underpin movement is thus crucial for predicting both small-scale ecological interactions and large-scale population patterns, which are foundational to ecological and evolutionary theory.

Life History Transitions

Across life-history stages, individuals encounter differing environmental conditions and novel challenges (Moran, 1994). The transition between these stages prompts the emergence of distinct behavioural traits within individuals (Cheron et al., 2021; Del Giudice et al., 2009). Among life-history stages, the timing of early-life transitions has particularly far-reaching consequences on survival (Tarwater & Brawn, 2010; Warner et al., 2009). One example of life-history transition is the onset of natal dispersal that often marks the start of independence from parents (Clobert et al., 2012). Natal dispersal is an extended process consisting of three phases: emigration from the natal range, transience, and settlement in time for the first reproduction (Bowler & Benton, 2005; Clobert et al., 2001, 2012). Each phase is characterised by distinct behavioural patterns and motivations, which are influenced by different intrinsic and extrinsic factors (Baguette et al., 2013; Clobert et al., 2009). Prior to emigration, individuals are mainly bound to the natal range, only sometimes undertaking exploratory forays outside of its boundaries. This phase is characterised by significant improvement of locomotor- (Yoda et al., 2004), cognitive- (Buchanan et al., 2013) and social-skills (Fischer et al., 2017) over a relatively short period of time. During this period, juveniles are typically dependent on parental care, benefitting from protection and from local knowledge about the availability of resources (Bonte et al., 2012). After emigration, throughout transience, individuals move through the landscape in a more erratic way as they search for suitable foraging habitats and gather knowledge about potential settlement areas and mates (Delgado et al., 2009; Penteriani et al., 2011). Following settlement, individuals often show more restricted, central place movement behaviour, as they are usually bound to a den or nest locations (Moorcroft & Lewis, 2013; Orgeret et al., 2023). Due to the long-lasting changes the transitions between life stages can have, gaining a better understanding of the conditions that lead up to such decisions can provide valuable insight into later life fitness outcomes.

Ontogeny of movement behaviour

The ability to balance the costs and benefits of movement optimally is not inherent but is refined by practice and improved with experience over time (Derégnaucourt & d’Ettorre, 2022). Juveniles often start out moving inefficiently and gradually learn to make more informed decisions, through which they can better acquire resources and minimise risks associated with movement (e.g. Harel et al., 2016). The trajectory of this maturation process can vary highly between individuals, and this can have significant effects on timings of life-history transitions and an individuals’ fitness prospects (Rotics et al., 2021). For soaring birds, learning to make use of wind conditions effectively is critical, as making effective use of thermal and orographic uplifts allows birds to minimise the energetic requirements of flight (Becciu et al., 2018; Hedenstrom, 1993) and expand the potential area they can access (Nourani et al., 2024). Furthermore, by learning to use wind resources effectively, maturing birds can also achieve higher travel speeds, allowing them to invest more time into other behaviours such as foraging (Yoda et al., 2004). Juveniles learn the basic blueprint for these skills in early life, however, their ability to hone these behaviours throughout their lifetime is key (Sergio et al., 2022), and often is reflected by shifts in space use (Aikens et al., 2024; Nourani et al., 2024).

Early-life conditions

The conditions experienced during early life can have a strong impact on maturation trajectories and triggering individual behavioural variation (Van de Pol et al., 2006). During early development, individuals are particularly sensitive to external stimuli, making them susceptible to stress and adverse conditions, of which food deprivation is one of the most influential (Eyck et al., 2019). One the one hand, traits that can be affected include skeletal and muscle development (Brown & Hay, 2016; Lee et al., 2016), neurological functioning (Matthews et al., 2002) as well as the hormonal and immunological system (Cole et al., 2012). Even when some traits like body weight or size can be compensated for by an acceleration of growth—given that conditions improve later on—negative effects of early adversity often persist throughout the entire life (Lee et al., 2016; Metcalfe & Monaghan, 2001). On the other hand, early-life conditions can act on behavioural traits, thus shaping behavioural phenotypes (Sachser et al., 2018). Behavioural traits affected by early-life conditions can include the cognitive ability (Buchanan et al., 2013), exploratory behaviour (Pakkala et al., 2016), and competitiveness (Monaghan, 2008; Spencer & Verhulst, 2007) but also the timing of life-history events (Rotics et al., 2021). Research has shown that individuals who experience favourable early-life conditions are more likely to emigrate at the optimal time, survive transience, and recruit into high-quality territories (Van De Pol & Verhulst, 2006). Conversely, individuals who experience adverse early-life conditions may exhibit lower competitiveness than their peers and be forced to disperse prematurely or delay dispersal, both of which can lead to reduced fitness. Thus, early-life conditions have the potential to directly shape behavioural phenotypes, but also to trigger long-lasting behavioural adaptations over time and context.

The social environment

The occurrence and distribution of conspecifics in a landscape forms a social environment (Formica & Tuttle, 2009; Moore et al., 1997). Conditions such as dominance hierarchies, territoriality and information sharing networks determine how individuals will react to the presence of conspecifics, thereby, shaping movement and dispersal processes (Grenier-Potvin et al., 2021; Griesser et al., 2008; Hansen et al., 2024). Yet, the social environment is often overlooked, as obtaining suitable data on conspecific densities and their distributions is challenging (Wey et al., 2015). In territorial species, the presence of many breeding conspecifics often leads to high competition among breeders and younger individuals aiming to enter the breeding population. This competition can delay life-history transitions, prolong the period of transience (Whitfield et al., 2022) as well as increase mortality (Cubaynes et al., 2014). In many species, a delay of settlement can thereby result in a larger proportion of pre-breeders within the population. On the one hand, these pre-breeding individuals, who have yet to establish a territory, are a critical component of the population (Orgeret et al., 2023). While they can have negative effects on breeding success of territory holders (Carrete et al., 2006; Jenny, 1992), they can also buffer population fluctuations and thus ensure long-term population stability (Kokko & Sutherland, 1998; Lee et al., 2017; Penteriani et al., 2011). On the other hand, pre-breeders need to successfully master the highly competitive environment in order to recruit into the breeding population. While the importance of prebreeders for population dynamics is widely recognised, we still lack a comprehensive understanding of pre-breeder behaviour, movement patterns, and strategies, leaving a crucial gap in our knowledge of how individual variation could determine successful recruitment.

An integrative approach to study natal dispersal

The complexity of how early-life conditions, intrinsic traits, and the social environment can interact to affect behavioural variation across multiple life-history stages highlights the need for an integrative approach when studying animal movement (Webber et al., 2023). Ignoring key drivers of core life-history transitions or treating life-history stages as isolated events may result in biased conclusions about the mechanistic pathways throughout life (Sih et al., 2004). These interconnected processes play a crucial role in determining future traits, phenotypes, and fitness outcomes (Bowler & Benton, 2005; Hoset et al., 2011; Ronce, 2007). Studying the link between different phases of natal dispersal in the context of the social environments can thus provide valuable insights into how the natal environment can scale up to influence individual behavioural phenotypes.

1.1 Study species

I focussed my PhD research on unveiling individual variation in behavioural phenotypes across multiple life-history stages of juvenile golden eagles (*Aquila chrysaetos*) within central Europe. Golden eagles are soaring specialists that use environmental uplift to reduce the energetic costs of flight. They are widely distributed over the northern hemisphere and inhabit a variety of different habitats. Within central Europe, golden eagles are mainly restricted to mountainous habitats (Ellis et al., 2024). Juvenile golden eagles have an extended dependency period of multiple months, during which they mature complex behaviours (Watson, 2010). Their movement during the dependency period is largely restricted to the parental home range and they feed on carrion or freshly hunted prey provisioned by their parents (Jenny et al., 2024; Watson, 2010). Already documented in the 1990s, individual variation in emigration timing in the Alpine population is extremely high and can span over several months (Haller, 1996). During transience, pre-breeders cover large distances and transition from a mainly scavenging to active hunting lifestyle in older ages. The transience period in our study population significantly exceeds the age of sexual maturation (Jenny et al., 2024), which is estimated to be reached at four years in golden eagles, in contrast to low-density populations where golden eagles may start to settle at the age of two (Whitfield et al., 2022). The Alpine golden eagle population is estimated to harbour between 13’000 and 15’000 breeding pairs and breeding pair territories cover the entire Alpine space nearly seamlessly (Jenny et al., 2024). This high population density might not only affect recruitment but also amplify individual differences in behaviours due to competition, both with breeding pairs and with pre-breeding conspecifics. Thus, due to the high variation in emigration timing and the high population density, the Alpine golden eagle population provides an exceptional study system to investigate a potential effect of early-life conditions on individual variation in later movement and space-use behaviour.

1.2 General methods

I used multiple data sources to understand space-use and movement behaviour of juvenile golden eagles. Between 2017 and 2023, we equipped a total of 87 juvenile golden eagles (2017: 3, 2018: 11, 2019: 22, 2020: 26, 2021: 16, 2022: 9, 2023: 5) within the Central Alpine range (Austria: 7, Switzerland: 37, Germany: 5, Italy: 35, Slovenia: 3) with solar-powered biologging tags manufactured by e-obs GmbH (Munich, Germany).

Figure 1.2.1. Overview of field methods used to equip juveniles with tags. (A) Abseiling into the nests when the juveniles were c. 50 days old. (B-D) Nestlings were measured, ringed and equipped with solar powered e-obs GPS/ACC tags. (E) After handling, the nestlings were brought back to the nest.

Tagging took place between late June and mid-July when nestlings had an age of 50 ± 3 days old. We assessed the age based on the development of feathers. During tagging, we carried out a physical assessment of the juvenile, recording measurements including body weight, beak and claw length (figure 1.1). As backpack harnesses have been shown to impact flight performance in large soaring birds, we instead use a leg-loop harness system to minimise such impacts (Longarini et al., 2023). The tags recorded high resolution geolocation GPS as well as tri-axial accelerometer ACC data. As we used solar-powered tags, we had to adjust data sampling regimes to adapt for limited battery recharging during the winter months when daylength and solar radiation was low. ACC data were recorded at regularly spaced intervals, allowing the inference of exact behaviours. GPS data were in contrast recorded at intervals that varied depending on battery charge to maximise the lifetime of the battery. From these biologging data I was able to determine not only the location but also the behaviour of animals, and consequently derive the timing of life-history transitions. I further had access to a detailed dataset on the golden eagle social system that allowed me to investigate golden eagle movement in the context of conspecific.

1.3 Thesis outline

In my PhD thesis, I investigated the development of juvenile behaviour and movement in the context of natal dispersal. Using a saturated population of a territorial raptor species as a study system, I explored how early-life conditions and behavioural phenotypes influence not only the start of the natal dispersal process, but also behavioural phenotypes and movement characteristics during the subsequent transience period. Focusing on individual variation enabled me to contribute new knowledge about the processes that may lead to successful recruitment in the face of high intraspecific competition.

In **Chapter I,** I assessed body condition and activity levels in nestling golden eagles and investigated the effect on timing of fledging and carry-over effects on post fledging behavioural traits. Specifically, I wanted to understand whether nestling condition and activity could manifest as persistent behavioural phenotypes throughout the post-fledging period and affect the timing of emigration. I found that better body condition and higher activity in the nest carried over to higher activity and more exploratory behaviour in the post-fledging period. Nestlings with higher post-fledging activity subsequently emigrated earlier. These results demonstrate that the effects of early-life conditions carry-over multiple life stages, affect life-history transitions and likely shape permanent behavioural phenotypes.

In **Chapter II**, I focussed on behavioural variation in the post-fledging period. Specifically, I investigated how the interplay between early-life food conditions and the development of energy-efficient flight skills affects the timing of emigration. For this purpose, I derived behavioural classes from ACC data using a random forest algorithm that I trained on a ground-truthed dataset from falconry golden eagles. I quantified time budgets and related inter-individual behavioural differences to emigration timing. I found that increased flight efficiency—characterised by more time spent soaring versus flapping—as well as frequent feeding during the post-fledging period were both associated with early emigration, but that these effects were independent from one another. These findings suggest that favourable natal conditions, such as abundant food and favourable environmental uplift availability, enable juveniles to maximise energy intake and minimise expenditure, leading to earlier independence from parental care.

After establishing that favourable early-life conditions and increased flight efficiency accelerated emigration timing in golden eagles, in **Chapter III** I explored how movement and space use behaviour developed after juveniles emigrated from the natal range. I was specifically interested in understanding whether the timing of emigration was associated with the movement behaviour of pre-breeders navigating through the saturated population. Contrary to my initial expectation that pre-breeders reduce movement with age, I found that pre-breeders became more mobile over time, especially those individuals that emigrated early. These results suggest that emigration timing can translate behavioural variation expressed in early life to differences in movement behaviour during transience. The individual variation in mobility patterns throughout transience is likely reinforced by the dense social system in which early-life conditions facilitate to overcome agonistic behaviours of territorial birds.

In **Chapter IV**, I investigated the effects of territoriality in the saturated Alpine golden eagle population upon space use patterns of pre-breeding golden eagles during the transience period. Combining the tracking data of pre-breeding golden eagles with a detailed monitoring dataset of existing golden eagle territories in Switzerland allowed me to determine that pre-breeder remained integrated in the population but avoided areas in close proximity to territory centres. This effect was more pronounced during periods of area—restricted movements than when pre-breeders moved through the landscape. This suggests that the social environment highly affects the spatial distribution of young individuals during transience and therefore has a strong potential in driving recruitment processes.

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2. Chapter I

Cascading carry-over effects of early activity phenotypes in golden eagles

Svea-Sophie Zimmermann[a,b], Martin U. Grüebler[a], Julia S. Hatzl[a,c], Enrico Bassi[d,e], Kamran Safi[f], David Jenny[a], Matthias Tschumi[a,]

Illustration: Lara Gross

Author details

[a] Swiss Ornithological Institute, Sempach, Switzerland.

[b] Department of Wildlife Ecology and Management, University of Freiburg, Germany

[c] Department of Landscape Ecology, ETH Zürich, Switzerland.

[d] ERSAF Lombardia Direzione Parco Nazionale dello Stelvio, Bormio, Italy

[e] Vulture Conservation Foundation Advisory Board, Zurich, Switzerland.

[f] Department of Migration, Max Planck Institute for Animal Behaviour, Radolfzell, Germany.

E-mail addresses and ORCIDs of co-authors

S.-S. Zimmermann: svszimmermann@gmail.com; ORCID: 0000-0002-2911-1391
M. U. Grüebler: martin.gruebler@vogelwarte.ch; ORCID: 0000-0003-4468-8292
J. S. Hatzl: julia.hatzl@vogelwarte.ch; ORCID: 0000-0002-7915-9588
E. Bassi: enrico.bassi76@gmail.com; ORCID: 0000-0002-0698-4800
K. Safi: ksafi@ab.mpg.de; ORCID: 0000-0002-8418-6759
D. Jenny: david.jenny@vogelwarte.ch; ORCID: 0000-0003-3027-0004
M. Tschumi: matthias.tschumi@vogelwarte.ch; ORCID: 0000-0002-7991-7780

Key words

Natal dispersal, biologging, silver spoon effect, individual quality, exploration, skill development, ODBA, carry-over effects, accelerometer

Chapter Notes

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Authors contributions

S.-S.Z., M.T., M.U.G. and J.S.H conceived the idea. S.-S.Z., J.S.H., K.S., D.J., E.B., carried out the fieldwork. S.-S.Z. conducted the formal analysis. Methodology was developed by S.-S.Z., M.T., M.U.G., J.S.H., K.S., D.J.; S.-S.Z. wrote the first draft of the manuscript and all authors contributed substantially to the revisions.

2.1 Abstract

Early-life conditions can carry-over to affect the fitness of animals later in life. Although evidence for early-life effects is prevalent now, we have only a limited understanding of the cascade of carry-over effects from early to later life stages. Juvenile animals allocate a lot of their energy to develop behavioural skills for their future life. Thus, early behavioural phenotypes might play a significant role for the translation of early-life conditions over a series of life stages. Here, we used GPS and body-acceleration data of 35 juvenile golden eagles (*Aquila chrysaetos*) to investigate the association between nestling body condition and activity levels (ODBA), the relationship of nestling ODBA with the timing of fledging and post-fledging ODBA and finally the effects post-fledging ODBA on exploration (foray) behaviour and the timing of departure to dispersal. Our results show support for a positive correlation between high body condition and high activity levels in nestlings. Active nestlings fledged earlier and tended to be more active in the early post-fledging period. Increased post-fledging activity levels tended to correlate with a high numbers of pre-dispersal forays and a younger age at departure. Our results suggest that early-life conditions not only shape body condition but also the early activity phenotype of nestlings. The early activity phenotype can drive the timing of subsequent life-history transitions and is translated over the entire post-fledging period representing a key mechanism linking early-life conditions with future survival and reproduction. The accumulated differences associated with the early activity phenotype suggest far-reaching fitness consequences later in life.

2.2 Introduction

During ontogeny, most organisms transition between discrete life stages during which they are confronted with often fundamentally different environments (Moran, 1994). Early-life stages are characterised by high mortality (Clark & Martin, 2007), typically occurring just after transitioning from one life stage to another (Low & Pärt, 2009). Thereby survival is strongly affected by the early-life conditions experienced (Naef-Daenzer & Grüebler, 2016; Perrig, Grüebler, Keil, & Naef-Daenzer, 2017). However, early-life conditions can also drive the expression and development of individual traits and carry-over to later life stages, translating stage-specific trait expressions from one life stage to another (Moore & Martin, 2019). Such carry-over effects of early-life conditions can have crucial effects on stage-specific individual performance but also far-reaching consequences for population composition and persistence (Le Galliard, Clobert, & Ferrière, 2004; Lindström, 1999). In the last decades, research has provided fundamental insights into the prevalent associations between early-life conditions and fitness parameters in later life (Moore & Martin, 2019; Van de Pol, Bruinzeel, Heg, Van Der Jeugd, & Verhulst, 2006). However, such within-individual associations often consider only two points at the beginning and at the end of the entire ontogenetic trajectory, but the translation processes of early-life conditions over multiple life stages remain largely unexplored (but see (Low & Pärt, 2009)).

The mechanisms underlying carry-over effects of early-life conditions to later stages can be linked to physiological characteristics such as oxidative stress (Reichert et al., 2014), corticosterone levels (Catitti et al., 2022) or telomere length (Reichert et al., 2014). However, early-life conditions can also shape behavioural phenotypes (Catitti, Grüebler, Farine, & Kormann, 2024; Richardson et al., 2019). Thereby, we are becoming increasingly aware of natal legacies that affect future locomotor and cognitive abilities (Whiteside, Sage, & Madden, 2016), but also social traits (Catitti et al., 2024; Stamps, 2006). Although more and more studies show consistent behavioural phenotypes later in life (Catitti et al., 2024; Richardson et al., 2019; Sih, Bell, Johnson, & Ziemba, 2004), we still have limited understanding of the downstream effects of early behavioural differences over multiple life stages.

In altricial birds, fledging from the nest is one of the most fundamental life-history transitions, as it marks a crucial first step towards independence from the parents and initiates flight trough an unknown environment (Martin, Tobalske, Riordan, Case, & Dial, 2018). Growth, physiology and behaviours related to flight start to develop in the nest and developmental thresholds need to be reached for successful fledging (Cornell, Gibson, & Williams, 2017; Ruaux, Lumineau, & de Margerie, 2020). As the conditions experienced in the nest modulate the developmental trajectories of nestlings (Lindström, 1999), they were found to affect the timing of fledging (Radersma, Tinbergen, & Komdeur, 2011) and subsequent survival in the post-fledging period (Perrig et al., 2024). Recent findings suggest that conditions in the nest not only shape body condition, but also impact behavioural phenotypes (Catitti et al., 2024). It therefore appears likely that behavioural differences associated with body condition are responsible for the translation of conditions in the nest to individual differences in the post-fledging period.

Becoming independent and leaving the parental home-range after the post-fledging period (i.e. the start of natal dispersal, (Clobert, Baguette, Benton, & Bullock, 2012)) represents another fundamental life-history transition (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009). Juvenile development is often not terminated at fledging but continues into the post-fledging period (Chapter II; Cornell et al., 2017; Ruaux et al., 2020). Beyond morphological and physiological developments, birds need to improve behavioural skills such as locomotion or vigilance (Ruaux et al., 2020) and may gain information and experience by undertaking forays outside the parental territory (Clobert et al., 2009). As in the nestling period, developmental trajectories during the post-fledging period are expected to affect the timing of departure to dispersal (Weston, Whitfield, Travis, & Lambin, 2018), and behavioural differences carried over from the nestling period may considerably shape these trajectories. Thereby, the conditions experienced during the post-fledging period can further affect skill development and alter the differences carried over from the nestling period. The timing of departure is thus a complex decision affected by intrinsic developmental factors interacting with both the nestling environment and the post-fledging environment (Bowler & Benton, 2005; Clobert et al., 2009). While our understanding about the environmental factors affecting the timing of departure is increasing (Fattebert, Perrig, Naef-Daenzer, & Grüebler, 2019; Robles et al., 2022), the downstream effects of behavioural differences in the nest on departure to dispersal are not well established.

Behavioural differences are difficult to record for free-roaming species during the post-fledging period, particularly in species using large or poorly accessible areas. However, animal borne biologgers now allow to infer subtle differences in body movement that can inform about behavioural differences. For example, overall dynamic body acceleration (ODBA) (Wilson et al., 2006) inferred from accelerometers has been shown to produce reliable proxies for estimating activity-specific energy expenditure (Brown, Kays, Wikelski, Wilson, & Klimley, 2013). ODBA can thus be used to quantify individual differences in time investment into energy-demanding behaviours such as locomotor training in the nest or flight behaviours after fledging, and about their developmental trajectories throughout the two life stages (Brown et al., 2013; Rotics et al., 2021). Most importantly, biologgers allow for investigating carry-over effects of early-life activity levels to activity levels and movement behaviours in subsequent life stages (Rotics et al., 2021). Yet, the role of the nestling environment for the nestlings' activity level remains largely unexplored and early-life activity has rarely been tracked throughout multiple life-history stages and linked to the timing of dispersal.

Here, we investigate the associations and carry-over effects of nestling activity levels over two major life-history transitions in Alpine golden eagles (*Aquila chrysaetos*), accounting also for sex differences and for rough environmental factors of the parental territory. The Alpine golden eagle is a large territorial, non-migratory raptor which breeds in high-mountainous habitats (Jenny et al., 2024). Golden eagles largely rely on environmental energy for energy-efficient soaring flight (Watson, 2010). After fledging, golden eagles show an extensive post-fledging period where flight behaviours mature (Chapter II; Soutullo, Urios, Ferrer, & Peñarrubia, 2006) with large individual variation in the timing of permanent departure from the parental territories (Weston et al., 2018). First, we addressed whether individual activity levels in the nest correlate with nestling body condition, suggesting that activity differences reflect individual quality and developmental state. Second, we investigated the effect of nestling activity levels on timing of fledging, expecting that high activity levels result in early fledging. Third, we quantified the correlation between nestling activity levels and post-fledging activity levels, expecting that high activity levels in the nest translate to high activity levels after fledging. Finally, assuming that post-fledging activity levels reflect developmental trajectories of energy-demanding flight behaviours, we analysed the effect of post-fledging activity on post-fledging exploration behaviour and the timing of departure. With this study we provide novel insights into how early-life conditions affect behavioural variation downstream over two life-history transitions, with potentially far-reaching consequences for natal dispersal and recruitment.

2.3 Methods

Study species

The golden eagle (*Aquila chrysaetos*) is a long-lived, territorial apex predator. With an average size of 50 km², territories usually accommodate multiple nests on cliffs or less commonly on trees, which are used alternatingly for many years (Jenny et al., 2024; Watson, 2010). Generally, pairs raise one to two chicks per brood, but breeding frequency fluctuates among years and pairs (Jenny et al., 2024). Chicks fledge at an age of 60 to 85 days and are dependent on parental care for multiple months thereafter (Jenny et al., 2024; Watson, 2010) during which they are mainly raised on fresh meat of Alpine marmot (*Marmota marmota*), chamois (*Rupricapra rupricapra*), roe deer (*Capreolus capreolus*), mountain hare (*Lepus timidus*), and grouse species (*Tetraoninae*) (Haller, 1996; Jenny et al., 2024). During the post-fledging period, juveniles continuously increase to feed on carcasses (Haller, 1996). After departure from their parental territory, golden eagles spend multiple years in transience before trying to take over or establish a territory (Jenny et al., 2024; Watson, 2010; Whitfield et al., 2022). During transience, juveniles successively transition from a mainly scavenging to an active hunting strategy (Haller, 1996).

Study area

The study was carried out in the cross-national Alpine region covering eastern parts of Switzerland (Grisons) and north-eastern parts of Italy (Lombardy and South Tirol). The study area is characterised by a diverse topography of deep valleys and high mountain peaks with steep cliffs (Jenny et al., 2024). Forests often stretch along valley slopes up to elevations between 1’900 m and 2’300 m where they give way to open ground and vegetation dominated by grasses and heather. Golden eagle territories almost completely cover the Alpine range reaching high breeding densities (Jenny et al., 2024).

Tagging and tracking

Between 2017 and 2020, we equipped 35 juvenile golden eagles (2017: 2, 2018: 8, 2019: 18, 2020: 7) from 27 different territories with solar GSM-GPS-ACC loggers (e-obs Gmbh, Munich, Germany), using a leg-loop harness made of two-layered Teflon ribbon with a silicon core (to allow for relative elasticity of 20%). Tagging took place between late June and mid-July when nestlings were 52.3 ± 4.6 sd days old. The age of each nestling was calculated based on the hatching date that was assessed during brood monitoring. The combined weight of transmitters and harnesses of 70 g made up less than 3% of the birds' body mass (mean of 3.5 ± 0.5 sd kg at the time of tagging). In five territories, two siblings were tagged in the same nest; in two territories, single nestlings were tagged in the same nest but in two consecutive years and in one territory, single nestlings were tagged two years apart and in two different nests. In addition to tagging, we ringed, weighed and measured all the nestlings and collected feathers with blood quills for genetic sex identification.

Transmitters recorded GPS and tri-axial accelerometer (ACC) data from 04:00 to 17:00 UTC in summer (May-October) and 09:00 to 16:00 UTC in winter (November-April). GPS locations were recorded in 20-minute intervals. ACC data was recorded every five minutes in 7.9 second bursts, on three orthogonal axes resembling body planes (x, y, and z) at a frequency of 33.3 Hz (1188 bytes). All data recorded by the tags were transmitted to and stored at the movebank data repository (Kranstauber et al., 2011). For further analyses, GPS data was filtered to retain only the first data point for every hour.

Fledging, exploration and departure to dispersal

We defined the timing of fledging visually by identifying the first trajectory of consecutive GPS locations from the scattered GPS signal inaccuracies around the nest. We thus defined fledging time as the first timestamp of the trajectory leading away from the nest site. The age of fledging was then calculated by subtracting the hatching date from the date of fledging. To determine explorations and the onset of natal dispersal, we used a spatiotemporal threshold adapted from "Method 7" described in (Weston, Whitfield, Travis, & Lambin, 2013): First, we calculated centroids from a kernel smoothed intensity of point patterns (R-package 'spatstat', (Baddeley, Rubak, & Turner, 2015)) with a Gaussian kernel based on data between fledging and a preliminary date of emigration assessed subjectively by investigating the tracks. Around these centroids, we selected an 8 km radius as a distance threshold to fully include the juveniles' main home-range. The area within that threshold encompassed the juvenile home-range, favouring overestimation of smaller home-ranges to underestimation of large ones. Forays during the entire post-fledging period were defined as movements outside the circular home-range (minimum of one location) for a maximum duration of up to 14 days. The start of each foray was marked by the first location beyond the 8 km threshold, and the end point as the first subsequent location within the threshold. Adjustments were made based on visual examination of GPS tracks when a bird returned within the vicinity of > 6 km but < 8 km for no longer than two hours. In such a case, forays were counted as one instead of two. For each foray we calculated the duration in days and the maximum linear distance from the juvenile home-range centre in km. For the following statistical analyses, the number of forays was summed and the average duration of all forays, as well as the mean of all maximum distances calculated per individual during the entire post-fledging period. Departure to dispersal was defined as any movement outside the 8 km threshold without any overnight returns for more than 14 days (permanent departure) and the age at departure as the departure date minus the hatching date. Three of the 35 individuals were excluded from the foray and departure analysis as their tags either stopped transmitting (n = 2) or they left their parental territory only a few weeks after fledging (n = 1) without undertaking any forays.

Juvenile activity

We used overall dynamic body acceleration (ODBA) as a measure of activity (Wilson et al., 2006). We transformed the raw ACC data into gravitational force g and calculated ODBA for each 7.9 second long ACC burst using the package ‘moveACC’ (Scharf, 2018). We determined ODBA during the nestling period for the 11 days prior to fledging and for the first 45 days of the post-fledging period. The 45 days after fledging correspond to the time before individuals start undertaking regular forays and match with the duration of linear activity development (Weston et al., 2018). We calculated daily mean ODBA including recordings from 06:00-17:00 UTC and fitted two linear mixed-effects models to assess the effect of time on ODBA: (i) For the nestling period (11 days before fledging) and (ii) the early post-fledging period (45 days after fledging) we fitted a model each to assess the effect of sex and the relative number of days before and after fledging, respectively, on mean daily ODBA (table S1). The predictor “day” (i.e. number of days before or after fledging) was centred and scaled for each period and included as a fixed effect as well as the random slope for each individual. Derived from these models, we used the sex-corrected random intercepts as indicator for individual ODBA during each period (table S1; figure S1). Additionally, random slopes during the post-fledging period indicated the individual development of daily ODBA over time (table S1; figure S1). By standardising the predictor “day” for each period, the random intercepts represent the average ODBA for each period and individual bird. Days with data gaps of more than one full hour (n = 77 days from 12 individuals) and days with early forays undertaken before the first 45 days after fledging (n = 37 days from 14 individuals) were excluded and interpolated for these models.

Intrinsic and habitat variables

As a proxy for individual body condition, we calculated the deviation of recorded body mass from the mean body mass of males and females, respectively, to account for sexual dimorphism occurring in golden eagles (Bortolotti, 1984). We found no significant effect of age at tagging on body mass and the age of tagging was thus not accounted for to calculate body condition. Nest exposure was measured as compass degrees and translated into northness (degrees) and eastness (degrees) for the analyses. To calculate a proxy for parental habitat quality, we used yearly mean values of the normalized difference vegetation index (NDVI) per juvenile home range as an indicator for food availability via trophic cascades (Regos, Arenas-Castro, Tapia, Domínguez, & Honrado, 2021). To avoid overestimation of used space and foraging grounds, we calculated juvenile home ranges as 90% Minimum Convex Polygons (MCPs) using GPS points within the 8 km threshold defined above. During the post-fledging period, juvenile and parental home ranges are highly similar (Hemery, Duriez, Itty, Henry, & Besnard, 2024). As Golden eagles mostly forage in open areas which reflect their main prey’s preferred habitat (Jenny et al., 2024), forested areas were excluded (Forest Type 10 m High Resolution Layer derived from the Copernicus Land Monitoring Service). We extracted NDVI images using MODIS (Moderate Resolution Imaging Spectroradiometer) vegetation indices of the study area taken every 16 days from beginning of May 2017 to the end of April 2021 at 250 m resolution (ORNL DAAC, 2018) and cropped them to the extent of each juvenile home range in QGIS 3.18 (QGIS.org, 2021). We then used the cropped NDVI images to calculate yearly mean NDVI values for each pixel (250 m x 250 m) which we subsequently averaged over the entire home range. Negative NDVI values representing unvegetated areas were set to 0 to prevent a negative influence on overall means.

Statistical analysis

All statistical analyses were performed using R software version 4.0.5 (R Core Team, 2020). We fitted Bayesian linear mixed-effects models (LMM) and generalized linear mixed-effects models (GLMM) using package ‘rstanarm’ (Goodrich, Gabry, Ali, & Brilleman, 2022). To model nestling activity, we fitted an LMM for ODBA (random intercept of the ODBA model described above) during the nestling period as response variable, and nest exposure, NDVI, body condition and sex as fixed effects. Likewise, to model post-fledging activity, we fitted an LMM with post-fledging ODBA (random intercept of the ODBA model described above) as response variable and NDVI, sex and ODBA in the nest as fixed effects. The fledging age was modelled by fitting an LMM with nestling ODBA, nest exposition, body condition and sex as fixed effects. Foray patterns were assessed by fitting a Poisson GLMM for the number of forays and LMMs each for mean foray duration (square root-transformed) and mean maximum foray distance (log-transformed) as response variables with post-fledging ODBA, NDVI and sex as fixed effects. Finally, to assess factors influencing the individual age at departure, we fitted an LMM with post-fledging ODBA, NDVI, age at fledging and sex as fixed effects. To account for the non-independence of data between nestlings from the same brood or territory, as well as across years, territory, we included individual ID and year as crossed random effects in all models.

Explanatory variables were checked for collinearity using pairplots and Pearson’s correlation coefficient r. Because none of the explanatory variables showed a correlation of $r \geq 0.7$, all were retained in the models. In addition, all continuous explanatory variables were centred and scaled. Models were checked for convergence of the Markov chains with Brooks-Rubin-Gelman diagnostics (Brooks & Gelman, 1998) and for validity using posterior predictive checks (package ‘shinystan’; (Gabry, 2018)). Spatial autocorrelation in the residuals was checked using Moran’s I (package ‘ape’; (Paradis & Schliep, 2019)) and bubbleplots (package ‘sp’, (Pebesma & Bivand, 2005)) and no autocorrelation was detected. Models were created based on ecological hypotheses and no model selection was performed (cf. (Korner-Nievergelt et al., 2015)). Inference and predictions were based on simulated Bayesian posterior distributions using 10’000 simulations (4 chains of 5’000 iterations with a burn-in of 2’500 each). Additionally, posterior probabilities (PP) were calculated for all model estimates, indicating the probability of the estimates to differ from zero. Effects were considered to show strong support if PP ≥ 0.95 and some support (i.e. show a tendency) if 0.95 > PP > 0.9. Unless stated otherwise, model parameters and derived parameters are given as posterior means with 95% credible intervals (CrI).

2.4 Results

The nestlings weighted 3’524 ± 532 sd grams (range: 2’210 to 4’600 grams; N = 35) at tagging. Thereby females weighted 3’869 ± 460 sd grams (range: 2’880 to 4600 grams; N = 17) and males weighted 3’199 ± 368 sd grans (range: 2’210 to 3’700 grams; N = 19). Nestling ODBA in the 11 days prior to fledging was 0.06 ± 0.01 sd g (gravitational force; range: 0.03 to 0.08 g; N = 35) and increased to post-fledging ODBA of 0.08 ± 0.01 sd g (range: 0.06 to 0.10 g; N = 32) in the first 45 after fledging. Nestlings fledged at an age of 77.9 ± 6.2 sd days (range: 62 to 90 days; N = 35). All individuals undertook multiple forays (mean = 11.9 ± 6.7 sd forays; range 3 to 29; N = 32) during the post-fledging period before departing, lasting for 1.3 ± 1.0 sd days (range: 0.1 to 4.2 days; N = 32) directing them to areas in 22.4 ± 7.4 sd km (range: 13.3 to 137.2 km; N = 32) distance from the parental territory. No juveniles died between fledging and departure from the parental territory. Independence and thus, final departure from the parental territory occurred at an age of 280.6 ± 40.6 sd days (range: 185 to 328 days; N = 32).

Table 1. Estimates of the Linear Mixed Models investigating factors affecting nestling ODBA (11 days pre-fledging) and post-fledging ODBA (45 days post-fledging). Means (Estimates), 95% CrI and Bayesian posterior probabilities (PP) are given. Fixed effects with PP ≥ 0.95 are printed in bold; with 0.95 > PP > 0.9 in bold and italics. Nestling ODBA: n= 35 individuals from 27 territories. Post-fledging ODBA: n = 32 individuals from 26 territories. Standard deviations and 95% CrI of random effects are shown in table S2.

Model	**Fixed Effects**	**Estimates**	**95% CrI**	**PP (< or > 0)**
Nestling ODBA	Intercept	**0.052**	**0.041 to 0.061**	**1.000**
	Nest exposure (south)	*-0.001*	*-0.004 to 0.001*	*0.888*
	NDVI	< 0.000	-0.002 to 0.003	0.530
	Sex (male)	**0.003**	**-0.001 to 0.008**	**0.958**
	Body condition	***0.001***	***-0.001 to 0.004***	***0.913***
Post-fledging ODBA	Intercept	**0.077**	**0.067 to 0.085**	**1.000**
	Nestling ODBA	***0.005***	***-0.001 to 0.010***	***0.935***
	NDVI	0.001	-0.002 to 0.005	0.752
	Sex (male)	**0.005**	**-0.001 to 0.011**	**0.955**

Nestling period and fledging age

Nestling ODBA was not associated with the two environmental variables of the nest surrounding, nest exposition and NDVI (table 1). Instead, male nestlings showed higher ODBA than female nestlings. Accounting for environmental variables and sex, the model showed support for an effect of nestling condition on nestling ODBA. ODBA tended to be higher in nestlings in good body condition compared to nestlings in poor body condition (table 1, figure 1a).

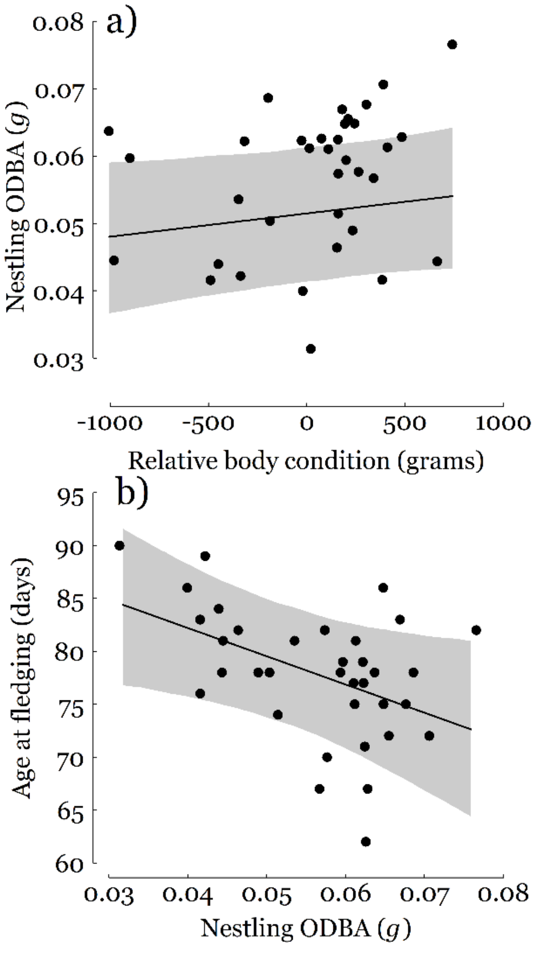

Figure 1. a) Nestling activity (average over 11 days pre-fledging; measured as ODBA in gravitational force *g*) of golden eagles in relation to nestling body condition (residuals from mean body weight of the respective sex in grams) and **b)** Age at fledging (in days from hatching) of golden eagle nestlings in relation to a) nestling activity (average over 11 days pre-fledging; measured as ODBA in gravitational force *g*). The solid line shows the mean and shaded areas 95% CrI of model predictions for females with all other model predictors set to their mean values. Filled circles show raw data points for both sexes. N = 35 individuals from 27 territories and four years.

Fledging age was strongly related to nestling ODBA and nest exposition. Nestlings with high ODBA fledged earlier than individuals with low ODBA (table 2, figure 1b) and individuals from southern exposed nests fledged earlier than individuals from northern exposed nests (table 2). When accounting for the effect of nestling ODBA, nestling body condition did not show an effect on fledging age. Yet male nestlings tended to fledge earlier than females in addition to their earlier fledging due to the increased ODBA (table 2).

Table 2. Estimates of the Linear Mixed Models investigating factors affecting age at fledging, exploratory behaviour (number of forays, Generalized Linear Mixed Model); foray duration (sqrt-transformed), foray distance (log-transformed)), and age at departure. Means (Estimates), 95% CrI and Bayesian posterior probabilities (PP) are given. Fixed effects with PP ≥ 0.95 are printed in bold; with 0.95 > PP > 0.9 in bold and italics. Age at fledging: n= 35 individuals from 27 territories; Forays and age at departure: n = 32 individuals from 26 territories. Standard deviations and 95% CrI of random effects are shown in table S2.

Model	**Fixed effects**	**Estimates**	**95% CrI**	**PP**
Age at fledging	Intercept	**78.433**	**72.932 to 84.129**	**1.000**
	Nestling ODBA	**-2.673**	**-5.123 to -0.196**	**0.984**
	Nest exposure (south)	**-2.187**	**-3.697 to -0.636**	**0.995**
	NDVI	0.029	-1.545 to 1.684	0.507
	Sex (male)	***-2.223***	***-5.391 to 0.787***	***0.928***
	Body condition	-0.817	-2.413 to 0.705	0.854
Number of forays	Intercept	**2.592**	**1.996 to 3.239**	**1.000**
	Post-fledging ODBA	***0.191***	***-0.090 to 0.471***	***0.919***
	NDVI	-0.009	-0.251 to 0.226	0.529
	Sex (male)	***-0.324***	***-0.736 to 0.070***	***0.944***
Mean foray duration	Intercept	**1.271**	**0.987 to 1.587**	**1.000**
	Post-fledging ODBA	-0.014	-0.159 to 0.189	0.561
	NDVI	-0.012	-0.150 to 0.176	0.561
	Sex (male)	**-0.342**	**-0.645 to -0.059**	**0.990**
Mean foray distance	Intercept	**3.228**	**3.030 to 3.434**	**1.000**
	Post-fledging ODBA	-0.016	-0.138 to 0.102	0.606
	NDVI	-0.006	-0.120 to 0.106	0.538
	Sex (male)	**-0.313**	**-0.530 to -0.098**	**0.998**
Age at departure	Intercept	**283.629**	**257.674 to 311.178**	**1.000**
	Post-fledging ODBA	***-10.787***	***-27.874 to 6.191***	***0.901***
	NDVI	-3.180	-20.087 to 14.143	0.656
	Sex (male)	-5.923	-32.433 to 20.087	0.687
	Age at fledging	***-12.150***	***-28.303 to 4.720***	***0.926***

Post-fledging period and departure

Although males tended to fledge earlier than females, females tended to undertake more forays after fledging than males (table 2). Females also spent more time and covered longer distances on individual forays than males (table 2). NDVI—indicative of food productivity of the parental territory—did neither affect foray behaviour nor age at departure (table 2). All individuals increased ODBA over the first 45 days post-fledging (table S1; figure S1). As in the nest, males also showed higher post-fledging ODBA than females (table 1).

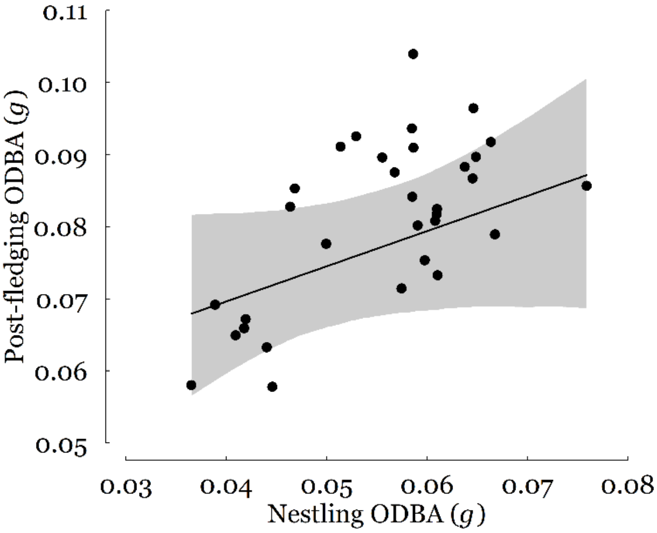

Figure 2. Post-fledging activity (over 45 days post-fledging; measured as ODBA in gravitational force *g*) of juvenile golden eagles in relation to their nestling activity (over 11 days pre-fledging; measured as ODBA in gravitational force *g*). The solid line shows the mean and the shaded area 95% CrI of model predictions for females with all other model predictors set to their mean values. Filled circles represent raw data points for both sexes. N = 32 individuals from 26 territories and four years.

In general, the model showed support for fledglings with high nestling ODBA also showing high post-fledging ODBA (table 1, figure 2). High post-fledging ODBA tended to be associated with an increased number of post-fledging forays, but not with the duration and distance of the forays (table 2, figure 3a). Fledglings with high post-fledging ODBA tended to also depart at a younger age than fledglings with a low ODBA (table 2; figure 3b). When accounting for this ODBA effect, juveniles that fledged later than their peers tended to depart after a shorter post-fledging period than their peers (table 2). Even though sexes slightly differed in fledging age and ODBA patterns, both in the nestling and the post-fledging period, males and females did not differ in their age at departure (table 2).

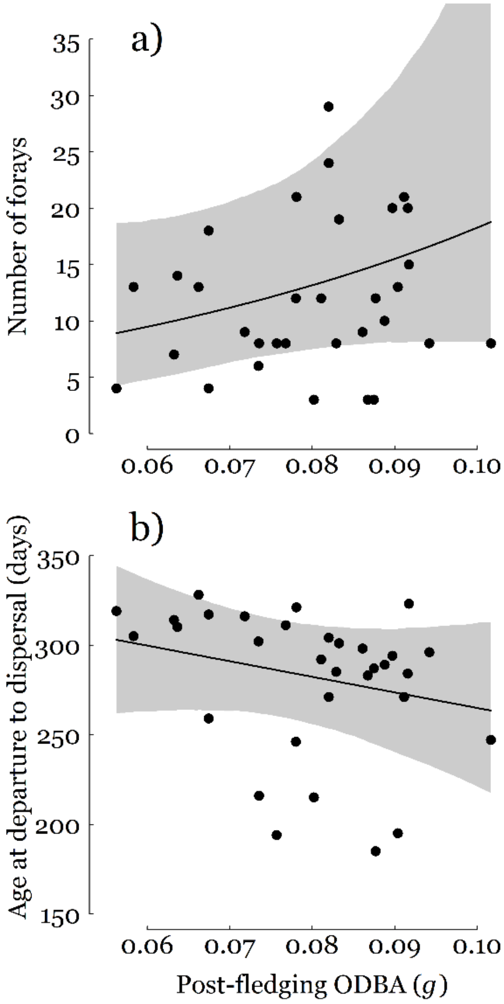

Figure 3. a) Number of forays and **b)** individual age at departure to dispersal of juvenile golden eagles in relation to post-fledging activity (over 45 days post-fledging; measured as ODBA in gravitational force *g*). The solid line shows the mean and the shaded area 95% CrI of model predictions for females with all other model predictors set to their mean values. Filled circles show raw data points for both sexes. N = 32 individuals from 26 territories and four years.

2.5 Discussion

Our results show evidence for an association between nestling condition and the nestlings' activity phenotype. This activity phenotype seems to persist in the post-fledging period with further effects on departure timing. These results suggest that juvenile golden eagles in good body condition were more active in the nest and that higher activity was associated with fledging at a younger age. More active nestlings continued to be more active during the post-fledging period, undertook more forays and ultimately departed earlier to dispersal. Our results provide novel insights into the correlational chain from the nestling period over the first life-history transition of fledging to the post-fledging period and further to the second life-history transition, the departure to dispersal.

Origin of the activity phenotype

Individuals with consistently higher activity levels likely show more behaviours associated with locomotion, both in the nest and in the early post-fledging period. In the nest, the set of behaviours include mainly energy-cheap behaviours, but nestlings increasingly walk, spread and flap wings when approaching the time of fledging (Ellis, 1979). Likewise, during the first weeks of the post-fledging period, birds allocate more and more time to flight at the expense of roosting Chapter II; Hemery et al., 2024). During ontogeny, high activity levels have been shown to reflect fast behavioural and skill development (Rotics et al., 2021) which is also supported in the juvenile golden eagles, where high mean post-fledging activity levels were associated with a steep increase of activity levels (Correlation between random intercept and random slope of ODBA: Pearson's $r = 0.90$). This implies that the activity phenotype not only reflects differences in flight propensity but also flight skill development.

The individual differences in activity levels, i.e. the activity phenotype expressed in the nest and in the post-fledging period, can arise from environmental conditions experienced in the nest (Pigeon et al., 2019) or from innate differences in the development of behaviours (Houdelier et al., 2011) as well as intrinsic tendencies to react to stimuli (Sih et al., 2004). The correlation of activity levels with body condition found in this study suggests that the activity phenotypes developed in the nest are at least partly driven by environmental conditions. The positive, though not very strong, correlation between high body condition and high activity in the nest suggests that well provisioned individuals can invest more time into movement behaviours. Yet, a large part of the variation in nestling activity remains unexplained, suggesting that physiological or developmental characteristics not directly related to the environment are likely to contribute to the observed behavioural phenotypes. The observed consistent sex-differences in activity levels, timing of fledging and exploration behaviour provide some support for innate differences in behavioural phenotypes. Based on a generally positive relationship of ODBA with body mass (Wilson et al., 2006), we would expect males, the smaller sex, to show lower activity levels than females. The inverse relationship observed here indicates that there are innate differences in activity between the sexes and/or that females need more time to physiologically develop to their larger size to be able to comparably use high-activity behaviour as males (Teather & Weatherhead, 1994; Weston et al., 2018).

The lack of effect of biomass productivity (NDVI) on activity levels, fledging age or movement characteristics at any stage investigated arguably provides further support for intrinsic behavioural differences. However, it is also possible that NDVI represents a poor proxy for environmental quality of natal territories in golden eagles. On one hand, it is conceivable that golden eagle prey abundance is not strongly linked to NDVI. This is underpinned by the lack of relationship between NDVI and nestling body condition (LMM, estimate: -84.5, 95% CrI: -245.2 to 79.5). On the other hand, other environmental factors such as the topographic configuration of territories and associated flight conditions may be more decisive for food accessibility (parental provisioning), juvenile flight propensity and locomotory development (cf. (Hemery et al., 2024)). Indeed, the prevailing energy landscape reflecting orographic and thermal conditions was recently shown to be associated with flight propensity and development in golden eagles (Nourani et al., 2024). The effect of nest exposure on the timing of fledging possibly corroborates the importance of topography and thermal conditions for behavioural development. Earlier fledging observed in more southern exposed nests could indicate that southern slopes offer improved flight conditions to parents for provisioning but possibly also to juveniles allowing them to fledge earlier. While these results suggest a combined effect of intrinsic and environmental effects driving flight activity and development, the direct and indirect contribution of specific factors deserves further investigation.

Carry-over of the activity phenotype

Golden eagle nestlings with high activity levels fledged early and tended to show high post-fledging activity levels. This suggests that the well-known link between nestling conditions and post-fledging survival (Cornell et al., 2017; Naef-Daenzer & Grüebler, 2016) is based on behavioural differences associated with nestling condition being preserved over the life-history transition of fledging. In long-lived species with high post-fledging survival such as the golden eagle (McIntyre & Collopy, 2006), the activity phenotype seems to carry-over to affect the behaviour in the entire post-fledging stage. Importantly, post-fledging activity levels tended to correlate with post-fledging exploration behaviour and with the start of dispersal. This implies that early-life conditions translate over multiple life-history transitions by affecting body condition and behavioural differences that shape a constant activity phenotype. While the conclusions regarding the origin of the activity phenotype in juvenile golden eagles remain limited, our study allows insights into the consistency of the activity phenotype between life stages and into its effect on the timing of fundamental life-history transitions. Carry-over effects of nestling body conditions on behaviour and fitness correlates later in life were often attributed to physiological conditions such as oxidative stress, corticosterone levels or telomere length (Catitti et al., 2022; Reichert et al., 2014). We now show that early-life conditions can also be reflected by the nestlings' activity phenotype and the behavioural differences underlying the activity phenotype can carry-over to later life stages. However, with this correlational study we cannot be sure whether the consistency in the activity phenotype between the two life stages is due to experiencing the same environment of the parental territory or due to consistence in behavioural traits irrespective into what environment the young birds fledge.

Forays outside the parental territory may be a beneficial move to attenuate the risks of dispersal: Forays allow individuals to obtain information on the surrounding environment and gain experience before leaving the parental territory permanently (Clobert et al., 2009). During forays, juveniles may assess the relative habitat quality of their natal range (Engler & Krone, 2021), practice to localise suitable feeding grounds and beneficial flight conditions (Bennetts & Kitchens, 2000), or learn to avoid agonistic behaviours of conspecific and anthropogenic threats once departed (Cozzi, Maag, Börger, Clutton-Brock, & Ozgul, 2018). More active juveniles may thus likely gain fitness benefits from undertaking more forays if the knowledge gain carries over to the dispersal phase.

Permanent departure from the natal area, finally, is a fundamental changepoint in the life of juvenile animals, as it entails leaving the known environment, the abrupt ending of parental care and concomitant shelter from predation or conspecific aggression (Clobert et al., 2009). This life-history transition to natal dispersal is thus risky and should only occur at a point when skills are developed to a degree that allow to deal with these costs (Bonte et al., 2012). The fact that individuals with high activity levels emigrated early suggests that there are benefits associated with early dispersal. These might include benefits for the detection and monopolisation of patchy food resources, the acquisition of high-quality temporary settlement areas or higher competitive ability in the social system (Clobert et al., 2012). We therefore expect that individuals with high activity phenotype experience also benefits after departure to dispersal due to both, benefits of increased activity and benefits of being earlier than their peers, and that these benefits ultimately provide benefits even later in life (cf. (Rotics et al., 2021)). The carry-over effect of activity differences from the nest to the post-fledging period and its subsequent translation to the start into the next life stage may have pursuing effects on post-dispersal stages (Catitti et al., 2024; Van de Pol et al., 2006). The accumulated differences associated with the high activity phenotype at departure may lower dispersal costs to increase survival (Bonte et al., 2012; Rotics et al., 2021), allow to more easily overcome energetic constraints of dispersal (Barbraud, Johnson, & Bertault, 2003; Robles et al., 2022), and facilitate an optimal dispersal outcome by increasing the likelihood of finding and settling in high-quality habitats early in life (Stamps, 2006; Van de Pol et al., 2006).

Conclusions

We found carry-over effects translating behaviours associated with early-life conditions over two life-history transitions. The well-known effect of early-life food conditions on nestling body condition (Catitti et al., 2022; Perrig, Grüebler, Keil, & Naef-Daenzer, 2014) was associated with an activity phenotype still present in the subsequent post-fledging life stage and carried over to affect timing of life-history transitions and movement decisions of juvenile birds. Our study therefore adds to the growing literature showing that behavioural phenotypes shaped by early-life conditions can persist and thereby represent a key mechanism linking early-life conditions with future survival and reproduction. ODBA derived from biologgers proofed to be suitable to quantify activity phenotypes. However, further research shedding light into the phenotypic variation in specific behaviours underlying the activity phenotype will refine our understanding of the behavioural mechanisms linking early-life conditions to individual fitness in long-lived animals and allow for better predictions of their population-level consequences.

2.6 Supporting information

Competing interests

We declare we have no competing interests.

Declaration of originality

We declare we came up with the research question, conducted the analysis wrote the full text ourselves.

Funding

We are grateful to the Walter & Bertha Gerber Foundation and Yvonne Jacob Foundation for their financial support and the Max Planck Institute for funding the tags and covering data transmission costs.

Ethical note

Handling, tagging and marking of golden eagle nestlings in Switzerland was carried out under the permit by the Food Safety and Veterinary Office Grisons (licence No. GR 2017_06, GR 2018_05E, GR 2019_03E). In Italy, the permissions for handling, tagging and marking were obtained from autonomous region of South Tyrol (Dekret 12257/2018 and Dekret 8788/2020), as well as from the Regione Lombardia and Sondrio Province for ringing and tagging in Lombardia and South Tyrol by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale) with the Richiesta di autorizzazione alla cattura di fauna selvatica per scopi scientifici (l.r. 26/93). All procedures followed the ASAB/ABS guidelines for the ethical treatment of animals in behavioural research and teaching and all applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The handling of birds was performed with maximum care and disturbance to nests kept to a minimum. Ethical approval for involving animals in this study was received through the application procedure for ringing permits and the scientific commission of the Swiss Ornithological Institute.

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2.8 Supplementary material

Table S1. Estimates of the Linear Mixed Models assessing the development of daily activity (ODBA in gravitational force *g*) in the 11 days before fledging (Individual daily nestling ODBA) and the 45 days after fledging (Individual daily post-fledging ODBA). Means (Estimates), 95% CrI and Bayesian posterior probabilities (PP) of fixed effects, as well as standard deviations (sd) and 95% Credible Intervals of random effects are given. Fixed effects with PP ≥ 0.95 are printed in bold; with 0.95 > PP > 0.9 in bold and italics. Individual daily nestling ODBA: n= 35 individuals; Individual daily post-fledging ODBA: n = 32 individuals.

Model	Fixed Effects	Estimates	95% CrI	PP (< or > 0)
Individual daily nestling ODBA	Intercept	**0.054**	**0.049 to 0.060**	**1.000**
	Day	0.0002	-0.002 to 0.002	0.600
	Sex (male)	0.004	-0.003 to 0.012	0.860
	sd Individual:day (Intercept)	$-1.541e^{-5}$	$-4.214e^{-5}$ to $6.172e^{-6}$	
	sd Individual:day (Slope)	$1.962e^{-5}$	$6.075e^{-6}$ to $4.168e^{-5}$	
Individual daily post-fledging ODBA	Intercept	**0.080**	**0.074 to 0.086**	**1.000**
	Day	**0.011**	**0.010 to 0.013**	**1.000**
	Sex (male)	0.002	-0.006 to 0.011	0.719
	sd Individual:day (Intercept)	$2.101e^{-5}$	$1.184e^{-6}$ to $4.791e^{-5}$	
	sd Individual:day (Slope)	$8.805e^{-6}$	$1.431e^{-6}$ to $2.267e^{-5}$	

Table S2. Standard deviations (sd) and 95% Credible Intervals of random effects for all models.

Model	**Random Effects**	**SD**	**95% CrI**
Nestling ODBA	Year	$9.22e^{-5}$	$1.81e^{-5}$ to $3.12e^{-4}$
	Territory ID	$1.17e^{-5}$	$1.39e^{-8}$ to $4.32e^{-5}$
Post-fledging ODBA	Year	$5.36e^{-5}$	$1.38e^{-8}$ to $2.58e^{-4}$
	Territory ID	$3.23e^{-5}$	$1.45e^{-7}$ to $8.75e^{-5}$
Age at fledging	Year	26.9	3.33 to 103.11
	Territory ID	2.46	0.00 to 12.14
Number of forays	Year	0.26	0.00 to 1.53
	Territory ID	0.26	0.10 to 0.54
Mean foray duration	Year	0.038	0.00 to 0.24
	Territory ID	0.08	0.00 to 0.21
Mean foray distance	Year	0.01	0.00 to 0.10
	Territory ID	0.02	0.00 to 0.07
Age at departure	Year	250.62	0.08 to 1667.76
	Territory ID	1211.08	92.11 to 2537.75

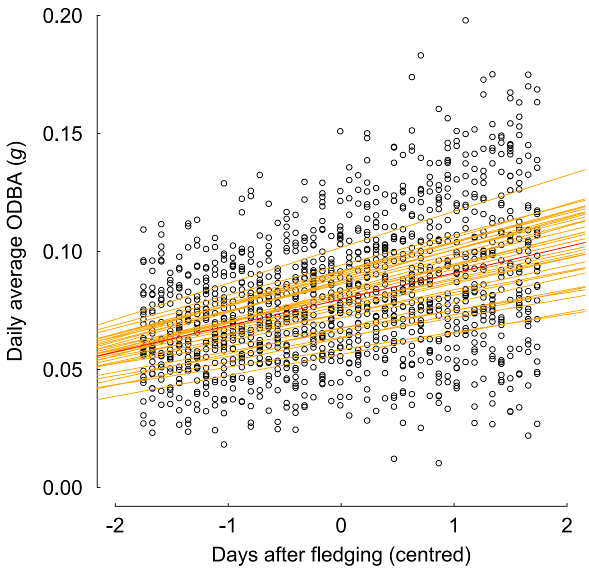

Figure S1. Development of individual daily activity (ODBA in gravitational force *g*) for all 32 individuals during the 45 days after fledging. Orange lines show individual regression lines and the red line the population mean of the standardised random intercepts and slopes of a linear mixed-effects model modelling individual ODBA in response to day after fledging and sex (table S1).

3. Chapter II

The consequences of food and flight efficiency for the timing of natal dispersal in golden eagles

Julia S. Hatzl [a, b], Matthias Tschumi [a], Enrico Bassi [c, d], Sam S. Cruickshank [e], David Jenny [a], Loïc Pellissier [b, f], Kamran Safi [g], Anne K. Scharf [g], Petra Sumasgutner [h], Martin U. Grüebler [a]

Illustration: Andrea Ritter

Author details

[a] Swiss Ornithological Institute, Sempach, Switzerland.

[b] Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland.

[c] Vulture Conservation Foundation Advisory Board, Zurich, Switzerland.

[d] Italian Ornithological Studies Center CISO

[e] Swiss National Park, Chastè Planta-Wildenberg, Zernez, Switzerland.

[f] Unit of Land Change Science, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland.

[g] Max Planck Institute of Animal Behavior, Radolfzell, Germany.

[h] Konrad Lorenz Research Center (KLF), Core Facility for Behavior and Cognition, Department of Behavioral and Cognitive Biology, University of Vienna, Grünau/Almtal, Austria.

E-mail addresses and ORCIDs of co-authors

J. S. Hatzl: julia.hatzl@vogelwarte.ch; ORCID: **0000-0002-7915-9588**
M. Tschumi: matthias.tschumi@vogelwarte.ch; ORCID: 0000-0002-7991-7780
E. Bassi: enrico.bassi76@gmail.com; ORCID: 0000-0002-0698-4800
S. S. Cruickshank: sam.cruickshank@nationalpark.ch; ORCID: 0000-0003-0183-5352
D. Jenny: jenny.d@compunet.ch; ORCID: 0000-0003-3027-0004
L. Pellissier: loic.pellissier@ethz.ch; ORCID: 0000-0002-2289-8259
K. Safi: ksafi@ab.mpg.de; ORCID: 0000-0002-8418-6759
A. K. Scharf: ascharf@ab.mpg.de; ORCHID: 0000-0002-3357-8533
P. Sumasgutner: petra.sumasgutner@univie.ac.at; ORCID: 0000-0001-7042-3461
M. U. Grüebler: martin.gruebler@vogelwarte.ch; ORCID: 0000-0003-4468-82

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Chapter notes

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Author Contribution

J.S.H., M.U.G., M.T. conceived the idea. J.S.H., K.S., D.J., S.S.C., E.B., P.S. carried out the fieldwork. J.S.H. conducted the formal analysis. Methodology was developed by J.S.H., M.U.G., M.T., A.K.S., L.P., K.S., P.S., D.J.; J.S.H. wrote the first draft of the manuscript and all authors contributed substantially to the revisions.

3.1 Abstract

The permanent emigration of a young animal from the natal range represents a critical life history transition. While early-life food conditions are known to be key determinants of emigration timing, the interplay between food conditions and the development of movement skills acting on emigration remains poorly understood. In this study, we investigated the effects of post-fledging flight and feeding behaviour on emigration timing in the Alpine golden eagle (*Aquila chrysaetos*), a large soaring raptor species. Increased post-fledging flight efficiency, characterised by the proportion of time spent soaring versus flapping, was associated with early emigration. Also, frequent feeding was associated with early emigration, but not with increased flight efficiency. These relationships suggest that favourable natal conditions during the early post-fledging period allow for maximising energy intake and minimising energy expenditure. Our results indicate that two environmental properties of the parental territory — food and environmental uplift availability — independently improve developmental rates, thereby allowing juveniles to emigrate early, which may confer future fitness benefits. Consequently, the availability of uplifts in the parental territory may represent an underappreciated driver for the maturation of juvenile soaring birds.

3.2 Introduction

Permanent emigration from the parental territory — the onset of natal dispersal — is a key transition in the life history of animals (Jean Clobert et al., 2009; Bowler & Benton, 2005). The timing of emigration is supposed to have strong implications for dispersal distance or settlement success and thus has consequences for lifetime reproduction and survival (Bonte et al., 2012; Mayer et al., 2017). Upon leaving their natal sites, juveniles lose benefits that accrue through site familiarity (Bonte et al., 2012). Nevertheless, they gain opportunities to capitalise on new resources (Stillman et al., 2022), gather information about potential breeding sites (Reed et al., 1999) and conspecifics (Jean Clobert et al., 2012), reduce kin competition (Matthysen, 2012), and eventually avoid inbreeding (Bowler and Benton, 2005; Behr et al., 2020). Therefore, emigration should occur when the benefits of leaving outweigh the costs of staying (Bonte et al., 2012). This cost-benefit trade-off is known to be modulated by habitat conditions experienced during early life (Scherler et al., 2023; Rémy et al., 2011), as well as by internal factors, such as sex (Edelman, 2011), body condition (Rémy et al., 2011) or the behavioural phenotype (Sih et al., 2004).

Social and behavioural skills acquired in early life can have long-lasting consequences (Langley et al., 2020; Turner et al., 2021), and the ability to learn specific skills might be of particular relevance for individual fitness (Langen, 1996). During the early life period, juveniles undergo significant locomotor developments and improve crucial movement skills such as predator escape (Hale, 1999), energy-efficient movement (de Grissac et al., 2017; Efrat et al. 2023; Rotics et al., 2016) and foraging behaviour (Corbeau et al., 2019). Individual variation in early locomotor skill development can therefore not only affect immediate performance and body condition, but also behaviour and survival much later in life (Henry & Ulijaszek, 1996; Lindström, 1999). In birds, many species use soaring and gliding to minimise their costs of flight by making use of thermal and orographic energy in the form of uplifts (Norberg, 1990; Williams et al., 2020; Corbeau et al., 2020). Since the energy expenditure of flapping flight increases proportionally with body mass (Hedenstrom, 1993), the use of low-cost soaring flight is particularly important for large and heavy birds. Although the development of soaring skills is likely to shape future performance of soaring birds, there are few studies investigating the consequences of individual variation in early soaring behaviours (Ferrer, 1992; Rotics et al., 2021), particularly because variation in post-fledging flight behaviours was hitherto difficult to quantify.

Differences in flight efficiency can drive the large variation in the timing of emigration between individuals of the same population. Birds are endowed with a genetic blueprint for flight, but flight often requires years of practice to fully mature (Harel et al., 2016; Ruaux et al., 2020; Yoda et al., 2004). Appropriate environmental conditions which facilitate uplifts thereby provide opportunities for practicing and honing the skills of extracting energy from atmospheric updrafts (Scacco et al., 2019). Recent literature suggests that even before emigration from natal territories, young birds can achieve ground speeds (Hemery et al., 2023) or cover daily distances comparable to adult birds (Weston et al., 2018). Yet, when it comes to marginal and challenging flight conditions, young soaring birds perform less well than experienced adults (Sergio et al., 2022; Harel et al., 2016; Nourani et al., 2024). Flying more efficiently may therefore facilitate early emigration, owing to the large effect differential flight efficiency has on energy expenditure.

How much energy an individual has available depends largely on how much food it gets. Limited food and poor nutrition during growth are linked not only to poor physical state but also reduced learning abilities (Brust et al., 2014). In birds, nestlings allocate most of their energy to growth (Flack et al., 2020). During the post-fledging period, the available energy in the form of food must be balanced to cover both the energetic costs of continued physical development (Bishop et al., 1996) and the costs of flight. Consequently, poor food availability can impair the development of movement during the post-fledging period (Whiteside et al., 2015; Scridel et al., 2023), resulting in a reduced ability to escape predators (O'Hagan et al., 2015) or a limited neurocognitive performance (De Rooij et al., 2010). Investigating how food availability acts on the ontogenetic pathway after fledging can thus deepen our understanding of potential energy trade-offs throughout developmental processes.

The Alpine golden eagle (*Aquila chrysaetos*) represents an ideal model species to investigate the effect of post-fledging skill development on emigration timing. Golden eagles are specialised in soaring flight, have an extended post-fledging dependency period and show a highly variable emigration timing (Weston et al., 2013; Haller 1996; Zimmermann, 2021). During the parental care period juveniles are provided with food and protection from conspecific aggression (Jenny et al., 2024). They start to carry out independent forays into neighbouring territories prior to permanent emigration—more so if they also show high activity within the parental territory (Zimmermann, 2021; Weston et al., 2013). Thus, food-modulated differences in the development of energy-efficient flight behaviours can be an important driver of the ontogenetic trajectories to an independent life in golden eagles.

Here, we investigated how post-fledging feeding, i.e. energy intake, and post-fledging energy investment into flight behaviours affected the timing of permanent emigration from the parental territory in juvenile Alpine golden eagles. To this end, we quantified the between-individual variation in the temporal development of—as well as the total time investment into—both flight and feeding behaviours using accelerometer data. First, we analysed the development of flight efficiency in terms of the time invested into soaring versus flapping flight, expecting that individuals become more efficient in flight with age by increasing the share of soaring in the total flight time. Second, we investigated whether individual variation in the development of flight efficiency was associated with emigration timing, expecting that individuals with a rapid development and high share of soaring flight emigrate early. Third, we explored whether the time spent feeding affected flight development or emigration timing. We expected that individuals that fed frequently had more energy available to invest in acquiring soaring skills than individuals feeding less often, thereby advancing emigration timing.

3.3 Methods

(a) Study species

The golden eagle is a large apex raptor species, highly adapted to make use of environmental energy in the form of orographic and thermal uplift for soaring flight. In central Europe, golden eagles are mostly restricted to the Alpine and Jura Mountain ranges (Haller, 1996). Territories include a mosaic of different habitats in which nests are built in rock cavities and less frequently in trees (Jenny et al., 2024). After a nestling period of c. 78 days, juveniles remain within the natal territory for several months after fledging (Haller, 1996; Zimmermann, 2021). Throughout this natal dependency period, juveniles are provided with freshly hunted prey and sometimes carrion by their parents. The main prey species include Alpine marmots (*Marmota marmota*), grouse species (*Tetrao tetrix, Lagopus muta*), as well as juvenile chamois (*Rupicapra rupicapra*) and ibex (*Capra ibex*). Carrion represents the primary food source of juvenile birds during the first years of independence (Haller, 1996).

(b) Data collection

We equipped juvenile golden eagles throughout the Alpine range with solar-powered biologging tags manufactured by e-obs GmbH (Munich, Germany). The tags recorded both location (GPS) and tri-axial accelerometer (ACC) data from which we derived the fledging and emigration time, as well as behavioural information. During 2018 – 2021, we tagged 36 nestlings (Switzerland: n = 27, Italy: n = 8, Germany: n = 1) at the age of 50 (±3) days using a leg-loop harness (Hegglin, Wehrle, & Aebischer, 2004). Combined tag and harness weight did not exceed 83 g, staying below 3 % of an individual's body weight for soaring birds (Kenward, 2001). ACC data were collected in bursts with a duration of 7.92 seconds at five-minute intervals between 04:00 and 17:00 UTC. Bursts were collected with a byte count of 1188 and a sample rate of 33.3 Hertz on all three axes within a detection range of ± 4 g (gravitational force $g = 9.81\ m\ s^{-2}$). The data were transmitted via GSM once a day and stored at movebank.org (Wikelski, Davidson, & Kays, 2022). For the molecular sex determination, DNA was extracted from the bottom (ca 3mm) of blood quills which were collected during the tagging event using the DNeasy blood and tissue extraction kit (Qiagen) per manufacturer's instructions.

(c) Behavioural validation

We used direct behavioural observations of tagged individuals to develop an algorithm that can detect patterns in ACC data and link them to behavioural classes (Nathan et al., 2012). We obtained simultaneous behavioural and ACC data (i.e., a ground-truthed dataset) by recording ACC data and behavioural information from free-flying falconry golden eagles (Rast et al., 2020). Six golden eagles at the Adler-Arena Burg Landskron, Austria, were fitted with the same tags (n = 12) and leg-loop attachment system as we fitted to the wild golden eagles. We used a Velcro attachment for the tag which allowed for the removal and exchange of tags between individuals. This tag exchange allowed us to mitigate the impact of individual variation in logger positions between birds. Each bird flew with at least three different tags, resulting in a total of 62 independent flights and 6610 ACC bursts. ACC data were recorded with the same settings as in wild individuals, but with a shorter interval of one second in between bursts to maximise data collection. We recorded golden eagle behaviour using video footage with audio comments (Canon Inc. EOS R5 camera and a Canon Inc. EF 100-400mm f/4.5-5.6L IS II USM lens). We annotated behavioural classes to video sequences following a predefined behavioural ethogram using the software Solomon Coder (Version: beta 19.08.02) and matched behaviours to the corresponding ACC burst according to time stamps. Tags were set to record data in GPS time for which we had to correct by 18 leap seconds to match UTC time (year 2020). If multiple behaviours were present in a burst, the respective bursts were assigned to the longest cumulative behaviour (cf. (Sur et al., 2017)). We excluded behaviours with less than 20 bursts (N = 45 bursts), bursts that contained unnatural behaviours (e.g. bird being handled by the falconer, N = 1'010 bursts), bursts where the cumulative extent of a behavioural category did not contribute to more than half of the duration (n = 121 bursts) and bursts that contained more than 2 unique behaviours (n = 379 bursts) from subsequent analyses (Sur et al., 2017). To reduce the effect of unequal sample size between behavioural classes, we randomly subsampled overrepresented classes to a maximum of 200 samples per class. This resulted in 1012 bursts and 7 behavioural classes (food intake, soaring flight, flapping flight, undulating flight, roosting, preening, and walking) in the ground-truthed falconry dataset ('FALCONRY') used for training and testing the classification algorithm.

In addition to the ‘FALCONRY’ dataset, we collected 181 ground-truthed ACC bursts of 12 tagged wild golden eagles (‘WILD’). This dataset allowed us to verify that the machine learning procedure we used to train the classification with falconry golden eagle data performed well in identifying behaviours of wild golden eagles. Additionally, it enabled us to assess how generalisable the algorithm was to data from new individuals (individual selected testing data) to reduce overestimation of classification accuracy (Dickinson et al., 2021; Ferdinandy et al., 2020). We located tagged individuals in the field using their most recent available GPS data and VHF signal and used the same behavioural classification protocol as for falconry golden eagles during observations in the field.

(d) Behavioural classification

All analyses were performed using the software R version 4.0.0 (R Core Team, 2020). We downloaded ACC data from movebank.org using the package ‘move’ version 4.1.12 (Kranstauber et al., 2017) and used a random forest algorithm to identify behavioural classes in ACC data (Nathan et al., 2012; Tatler, Cassey, & Prowse, 2018) using the package 'randomForest’ version 4.6-14 (Liaw & Wiener, 2002). Random forests are widely used for classification of behaviours from ACC data and are based on a hierarchical decision rule structure (Cutler et al., 2007). We extracted 58 descriptive ACC features from each ACC burst using an adapted function within the package ‘moveACC’ version 0.1 (Scharf, 2021). Features extracted per ACC axis included minimum, maximum and mean values, standard deviation, skewness, kurtosis, mean dynamic acceleration, temporal autocorrelation, and the trend. Pairwise-calculated features consisted of the correlation between axes as well as the sum of how often two axes crossed each other. In addition, we calculated the mean overall dynamic body acceleration ODBA (Wilson et al., 2006) and its standard deviation, derived dominant amplitude and frequency measures using a Fast Fourier Transformation, and used the variation explained by the first three principal components of a Principal Component Analysis, as well as pitch and roll angle (electronic supplementary material, table S1). We split the ‘FALCONRY‘ dataset into a training subset (80% of the data per class) and a testing subset (remaining 20%) and trained the algorithm using the training subset. We grew 2500 trees and used 9 variables at each split using the package ‘caret’ version 6.0-88 (Kuhn, 2008). To improve model performance, we used repeated cross-validation with 10 repeats and up-sampled rare classes to help reduce the effect of the remaining class imbalances. Using this model, we predicted behavioural classes in the testing subset of the ‘FALCONRY’ data, as well as of the ‘WILD’ dataset. We then compared predicted vs. observed classes using a confusion matrix to evaluate accuracy, class-specific balanced accuracy, sensitivity, and specificity.

(e) Time budget analysis

We modelled the daily frequencies of behaviourally classified ACC data in free ranging eagles over the 45 days following fledging to quantify the time spent in different behaviours during the early post fledging period. This time period was chosen as it is the period in which activity has been shown to develop linearly (Weston et al. 2018) but before the time when individuals start making excursions. To analyse the effect of sex and time since fledging on time allocation to behavioural classes, we fitted a Bayesian multilevel multinomial model using the package ‘brms’ version 2.16.10 (Bürkner, 2021) to the 209’487 classified accelerometer bursts (Bürkner, 2021; Koster & McElreath, 2017). The model allowed us to capture the multinomial nature of time-budget data while accounting for both fixed and random effects. We modelled the proportion of bursts of each behaviour in relation to the time since fledging (in days, 1-45 days after fledging), the quadratic term of time since fledging (orthogonal to day), and sex (females n = 19; males n = 17) as fixed effects and applied a logit-link function. We determined fledging- (permanent departure from the nest) and emigration- dates (permanent departure from the parental territory) following a distance threshold approach described in (Zimmermann, 2021). Explanatory variables were checked for collinearity using pair plots and Spearman’s rank correlation coefficient ‘rho’. As no correlation was present (rho ≤ 0.6), all variables were retained in the model. Date (220 levels) and individual ID (36 levels) were included as random intercepts to account for non-independence of data collected on the same date and from the same individual. Furthermore, we allowed for individual-specific variation in the linear effect of day (random slope). We extracted and standardised the individual-specific random intercepts and slopes to use them for further analyses of behaviours.

We ran four chains of 7’000 iterations, of which we discarded 3’500 as burn-in and used the remaining iterations to derive the posterior distribution of the model parameters. As recommended by Gelman (2006), we used weakly informative, normally distributed priors (0, 5) for population level effects and adapted the maximum tree depth to 15 to improve effective sample size for high dimensional models. We calculated posterior predictions from which we derived means and 95 % credible intervals for fixed effects in different behavioural classes, while holding all other coefficients constant (Koster & McElreath, 2017). To ascertain chain convergence, we used Rhat-values, effective sample sizes and posterior predictive checks (Brooks & Gelman, 1998).

(f) Flight behaviour and emigration models

To investigate the effect of the time spent feeding on the time spent in soaring and flapping flight, as well as on the increase rate of both flight behaviours, we used the standardised individual-specific random intercepts and slopes from the multinomial model. The standardised individual-specific intercept and slope of behavioural proportions over the 45 days allowed for the discrimination between (1) the individual steepness of increase or decrease of behaviours over the time period investigated (slope), and (2) the individual total time engaged in a behaviour throughout the time period (intercept) (electronic supplementary material, figure S1). We ran four linear-mixed effects models (package lme4; (Bates et al., 2015)) with (i) the individual-specific random intercept of soaring flight, (ii) the individual-specific random slope of soaring flight, (iii) the individual-specific random intercept of flapping flight and (iv) the individual-specific random slope of flapping flight as response variables, and the individual-specific intercept of food intake as a fixed explanatory variable to understand the effect of time engaged in food intake on the expression of flight behaviours.

We further explored the relationships between behavioural variation and emigration timing by fitting a linear mixed-effects model. The response variable was age at emigration (defined as days after fledging, with day of fledging set to zero), with individual-specific intercepts and slopes of soaring and flapping flight, the individual-specific intercept of feeding, and sex as fixed effects. We ran each model 14’000 times to account for the random intercept and slope errors from the multinomial model, selecting one random draw from the posterior distribution each time. Inferences were based on means, credible intervals and posterior probabilities across all draws. All numerical explanatory variables were z-transformed for better convergence and comparisons between variables. We excluded six individuals from the emigration model as data transmission ceased prior to emigration (n = 4) or emigration occurred earlier than 80 days post fledging—most probably due to disappearance of one of the parents from the territory (pers. communication Fankhuser Thomas). Effects with a posterior probability above 0.95 were considered significant.

3.4 Results

(a) Post-fledging behaviours

Validation of the classification algorithm using the two datasets showed that all behaviours except undulating flight could be reliably identified. The overall classification accuracy in the ‘FALCONRY’ dataset was marginally higher (92%) than in the ‘WILD’ dataset (87%). Class-specific balanced accuracy was relatively low for undulating flight (‘FALCONRY’: 88%, ‘WILD’: 50%) but ranged from 72% to 98% for all other behaviours in both datasets (electronic supplementary material, tables S2 and S3). The model identified the most important variables for distinguishing between behavioural classes to be the “mean of the z and y axes” and “pitch” (electronic supplementary material, figure S2).

During the first 45 days of their post-fledging period, juvenile golden eagles spent the majority of their time roosting (69.62%; 143’765 bursts) and preening (12.93%; 26’698), followed by feeding (9.43%; 19’462) and walking (2.24%; 4’621). Flight behaviours contributed comparably little to the overall time budget, with soaring shown in 8,301 bursts (4.02%), flapping in 3,383 bursts (1.64%) and undulating in 257 bursts (0.12%). However, the behavioural composition changed considerably over time (electronic supplementary material, table S4). With time since fledging, birds spent decreasing amounts of time roosting, preening and walking, whereas flapping and soaring flights became more frequent (figure 2; electronic supplementary material, figure S3). In addition, time spent in soaring flight increased faster than time spent in flapping flight (figure 2; electronic supplementary material, figure S3). Time spent soaring increased by a factor of eleven and reached 5.4% (95% CrI = 3.7% — 7.38%) at the end of the 45-day period, whereas time spent flapping only increased by a factor of seven and reached 2.3% (95% CrI = 1.75% — 2.96%). Time spent soaring was positively correlated with the time spent flapping (Pearson correlation coefficient r = 0.67). Time spent feeding increased from 8% (95% CrI = 6.66% — 9.37%) to 9.6% (95% CrI = 8.53% — 10.75%, figure 1) and decreased again to 8% thereafter. Roosting remained the dominant behaviour throughout the 45 days.

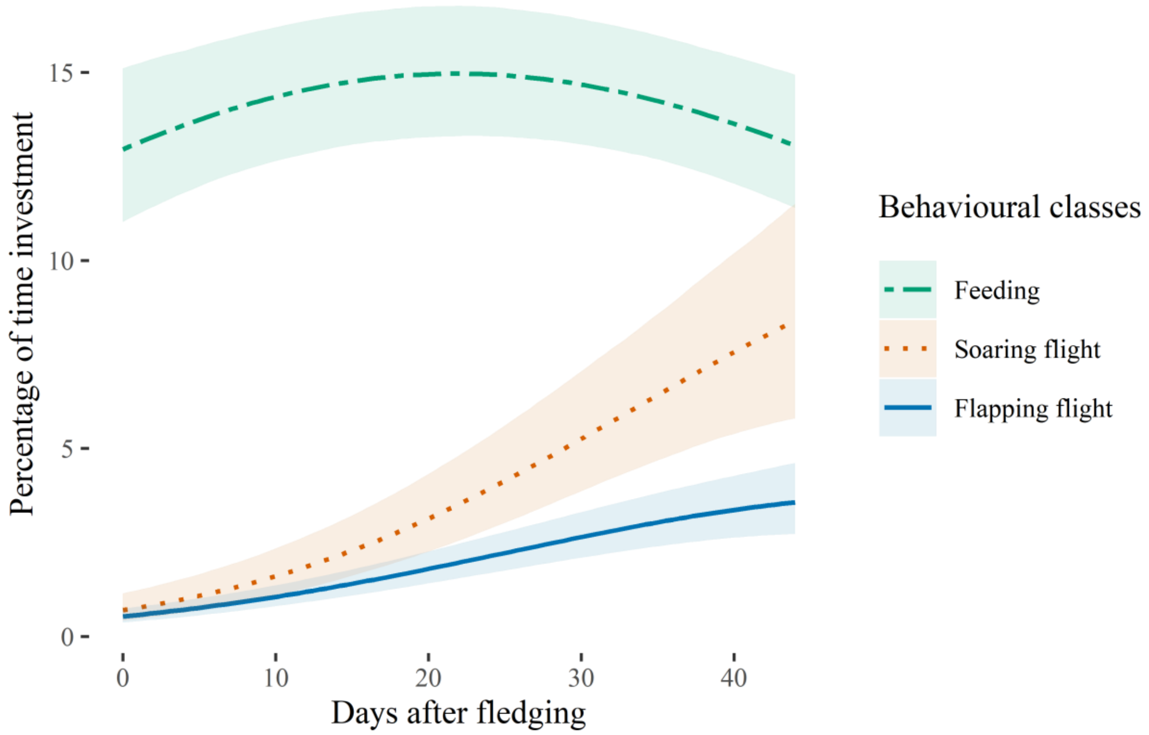

Figure 1. Change in the percentage of the time invested into feeding (green; dotdash), soaring flight (orange; dot), and flapping flight (blue; solid) during the first 45 days after fledging. Lines represent means and shaded areas indicate 95% credible intervals from model predictions for females.

Undulating flight showed the highest overall body acceleration ODBA (mean = 0.77 gravitational force g, 95% CI = 0.45 —1.27 g), followed by flapping flight (mean = 0.69 g, 95% CI = 0.34 — 1.23 g). Soaring flight had a considerably lower ODBA than the other two flight behaviours (mean = 0.23 g, 95% CI = 0.11 — 0.40 g) and was closer in ODBA to feeding (mean = 0.20 g, 95% CI = 0.08 — 0.40 g). With a mean of 0.02 g (95% CI = 0.01 — 0.07 g), roosting had by far the lowest ODBA. Over the 45 days, ODBA per burst decreased slightly but significantly for soaring bursts (Estimate = -0.005; CI: -0.07 — -0.003; PP = 1.00) and considerably for flapping bursts (Estimate = -0.068; CI: -0.081 — -0.055; PP = 1.00) but not for feeding bursts (Estimate = -0.006; CI: -0.001 — -0.01; PP = 0.96), indicating an increase in efficiency for soaring and flapping flight, but not for feeding behaviour. The daily sum of ODBA for soaring increased from 0.17 g (95% CI = 0.11 — 0.27 g) at day 1 to 1.83 g (95% CI = 1.26 — 2.51 g) at day 45 and for flapping from 0.41 g (95% CI = 0.29 — 0.57 g) to 2.07 g (95% CI = 1.58 — 2.68 g). Average ODBA per flight burst (including both soaring and flapping flight bursts) decreased from 0.47 g to 0.33 g during the 45 days post-fledging, a reduction of 30%, suggesting that flight became less demanding due to both an increase in flight efficiency and a higher share of soaring. The proportion of time spent preening, walking, and flapping differed between sexes (electronic supplementary material, table S4) with males investing more time in preening, walking, and flapping compared to females.

(b) Effect of time spent feeding on flight behaviours

Flapping and soaring flight were not related to the time spent feeding (table 1), neither in terms of the total time spent flying (individual-specific random intercept), nor in terms of the increase rate of time spent flying (individual-specific random slope).

Table 1. Estimates of linear models investigating the relationship between the time spent feeding and characteristics of flight behaviours. All variables represent individual-specific random intercepts (time spent) and slopes (increase rate) derived from the multinomial model assessing time budgets (electronic supplementary material, table S4). Shown are parameter means (Estimate), 95% credible intervals (95% CrI), and posterior probabilities (PP) derived from random draws of 14’000 linear mixed-effects models. Effects with a posterior probability ≥ 0.95 are printed in bold.

		Estimate	95% CrI	PP (> or < 0)
Increase of soaring	**Intercept**	**6.01**	**-0.42 to 13.79**	**0.97**
	Time spent feeding	1.22	-3.93 to 6.23	0.69
Time spent soaring	Intercept	-0.08	-0.36 to 0.19	0.70
	Time spent feeding	0.10	-0.10 to 0.30	0.85
Increase of flapping	Intercept	1.82	-2.10 to 6.19	0.81
	Time spent feeding	1.61	-2.01 to 5.41	0.81
Time spent flapping	Intercept	-0.02	-0.22 to 0.19	0.56
	Time spent feeding	0.10	-0.07 to 0.26	0.88

(c) Effect of flight and feeding behaviours on emigration

Individuals emigrated permanently from the natal territory at a mean of 199 ± 40 days (range = 103 to 254 days, n = 30) after fledging. Consequently, as most juveniles fledged at the end of July, 70% of individuals emigrated between February and March. Juveniles that spent more time soaring emigrated earlier than juveniles soaring less (table 2; figure 2a). Also, juveniles who spent more time feeding left their natal territories sooner than those who spent less time feeding (table 2; figure 2b).

Table 2. Estimates of the model investigating factors affecting the timing of emigration. Shown are parameter means (Estimate), 95% credible intervals (95% CrI), and posterior probabilities (PP) derived from random draws of 14’000 linear mixed-effects models. The models used the posterior draws of the random effects extracted from the multinomial model. Effects with a posterior probability ≥ 0.95 are printed in bold.

	Estimate	95% CrI	PP (> or < 0)
Intercept	**195.22**	**169.04 to 221.59**	**1.00**
Time spent flapping	17.70	-5.62 to 41.80	0.93
Increase of flapping	5.20	-14.99 to 25.79	0.70
Time spent soaring	**-23.88**	**-47.33 to -0.51**	**0.98**
Increase of soaring	-4.81	-24.63 to 14.42	0.69
Time spent feeding	**-16.27**	**-33.74 to 1.49**	**0.97**
Sex (male)	6.10	-33.67 to 45.80	0.63

After accounting for the effects of soaring and feeding behaviour, individuals that spent more time in flapping flight tended to emigrate later than individuals flapping less often (figure 2c). Males and females did not differ in their timing of emigration (table 2). The results of the same model but including the four individuals that emigrated earlier than 80 days post fledging, were qualitatively similar. However, the effect sizes and effect certainties of soaring time and flapping time were reduced (electronic supplementary material, table S5).

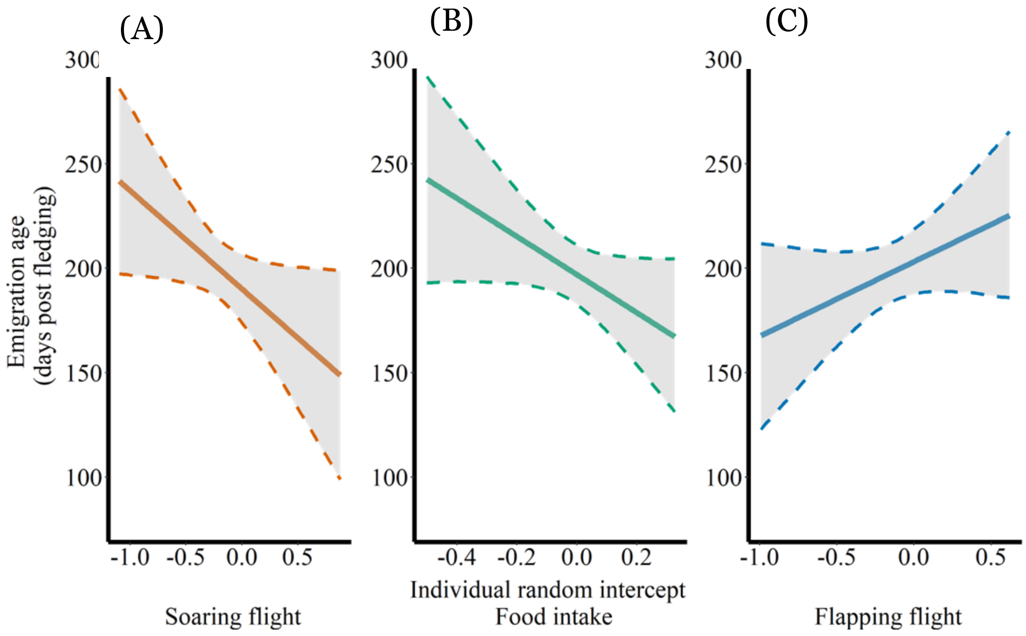

Figure 2. Effects of time investment into (A) soaring, (B) feeding, and (C) flapping on emigration age. The solid line shows the mean and the dashed lines the 95% credible intervals from model predictions for females.

3.5 Discussion

We show that conditions during the early post-fledging period had drastic effects on the decisions juvenile golden eagles made months later in their life. Quantifying between-individual variation in feeding and flight behaviours enabled us to investigate the effects of energy intake and energy expenditure upon the onset of independence from parental care and start of natal dispersal. Our results indicate that increased flight efficiency in terms of an increased soaring - flapping ratio was associated with early emigration from the natal territory. We also found that much time engaged in feeding advanced emigration, but that the time spent feeding had no effect on the expression of flight behaviours. Our results therefore suggest that post-fledging food availability had only a limited effect on flight skill development in golden eagles. Yet, both high food availability and favourable flight conditions accelerated the maturation process independently from one another and advanced the onset of natal dispersal.

(a) Post-fledging development of flight skills and efficiency

In general, juvenile golden eagles improved flight efficiency rapidly after leaving the nest. By increasing the use of soaring flight, juveniles presumably reduced the flight costs by c. 30 % during the first 45 days after fledging. This was possible because flapping flight showed a three-fold higher overall dynamic body acceleration ODBA (Wilson et al., 2006) than soaring flight, which is in line with the current state of knowledge (Duriez et al., 2014; Norberg, 1990; Scacco et al., 2023). Being able to quickly reduce flight costs likely allowed juveniles to reduce energetic requirements associated with movement, therefore freeing up energy for other aspects of ontogeny. The freed-up energy can be used for building up experience (Corbeau et al., 2020), enhancing memory (Ramsaran et al., 2019) and cognitive performance (Thornton & Lukas, 2012). Our results at the population level therefore suggest that the early change to a predominant use of soaring flight is important for the further development of skills towards independence. Because of the crucial implications of energy efficient movement on the energy budget, a rapid development of flight efficiency can even take ontogenetic priority over other physical or behavioural developments when resources are limited (Berghänel, Schülke, & Ostner, 2015). Especially in golden eagles, where females are larger and heavier than males, benefit from lower wing loading as juveniles, which helps them to negotiate the aerial medium despite limited experience (Lish et al., 2016) very early in life. The increase in flight efficiency is shown to continue even far beyond emigration in soaring specialists (Efrat et al., 2023; Nourani et al., 2024), indicating that individual variation in early flight efficiency might also affect future flight skill developments.

(b) Effects of post-fledging flight behaviours on emigration timing

Despite the rapid acquisition of soaring skills, juvenile golden eagles showed large individual variation in the expression of post-fledging flight behaviours, and thus flight efficiency. The soaring – flapping ratio differed considerably between individuals, suggesting high variation in energy expenditure per unit time of flight. Juveniles showing a high flight efficiency emigrated earlier compared to their peers showing lower efficiency, indicating that energy efficient flight might be an important driver for becoming independent. Soaring birds with a lower share of soaring flight generally have low climb rates (Harel et al., 2016) and have disadvantages in foraging success (Navarro & González-Solís, 2007) or in venturing on exploratory foray flights outside the natal range to gather information (Poli et al., 2024). Low flight efficiency has also been shown to reduce survival of juvenile white storks during the first migration (Rotics et al., 2016). Yet, even well-skilled and experienced soaring birds have to use flapping flight occasionally for take-off and landing (Duriez et al., 2014; Williams et al., 2020), as well as for changing from one uplift to another (Williams et al., 2020). We therefore suggest that juvenile golden eagles with low-efficiency flight behaviour have difficulties staying in uplifts and thus can only sustain short periods of soaring. This would result in reduced flight elevations and travelling distances—especially when wind conditions are challenging—as well as potentially increased energetic costs when shifting between neighbouring uplifts (Harel et al., 2016). An improved ability to efficiently locate uplifts, fly at high altitudes, and achieve high climb rates clearly will provide juveniles with significant advantages in coping with the competitive environment post-emigration, in particular in our saturated Alpine golden eagle population. Thus, the benefits of post-fledging flight efficiency are likely to exceed the immediate energy savings during the post-fledging period. The early emigration then represents a possible mechanism to translate these benefits far into the post-emigration phase.

The speed at which flight skills developed might have been of lesser importance to our golden eagles than opportunities to practice. Our results show that individual differences in the total time invested into soaring, but not differences in the speed at which soaring is acquired (i.e. the slope of the change in soaring over time) correlated with the timing of emigration. Even though a more rapid skill development has been previously linked to better cognitive performance (Cadoret et al., 2018), increased foraging success (Raine & Chittka, 2008), and higher survival (Rotics et al., 2021), our results indicate that golden eagles were already equipped with a strong genetic blueprint for learning the basics of energy-efficient flight, as has been suggested for other soaring species (Corbeau et al., 2020). This is further supported by the fact that food intake had no effect on either flight skill development or the time spent flying. Instead, the sheer opportunity to practice soaring flight under favourable conditions might actually be the critical factor for developing the full array of abilities that enable early emigration from the parental territory. The local energetic conditions in the proximity of the nest, including static characteristics like exposition, slope, and ruggedness, as well as dynamic components including wind speed, direction, and solar radiation (Duriez et al., 2014; Scacco et al., 2019; Shepard et al., 2013), can strongly affect the costs of flight and also time invest into flight. Young golden eagles in particular rely more on orographic uplifts than on thermal uplifts (Bohrer et al., 2012) and birds develop the ability to exploit thermal uplift energy only later in life (Nourani et al., 2024). Therefore, the landscape, the territories themselves, and the prevailing uplift conditions are the main drivers of the time juveniles required to reach and exploit features of interest, such as vertical updrafts (Shepard et al., 2013; Williams et al., 2020) and areas of high prey or carcass abundance. Hence, the availability of easy-to-exploit uplifts in the parental territory could represent an underappreciated driver for the behavioural maturation after fledging in juvenile soaring birds. This might be particularly relevant for Alpine golden eagles, as emigration occurs in winter when uplift conditions are highly challenging (Nathan et al., 2012).

(c) Effects of post-fledging feeding behaviour on emigration timing

Although we observed no effect of differences in time spent feeding upon flight behaviours, individuals who fed more emigrated earlier. Favourable feeding conditions thus seem to provide advantages affecting maturation in addition to those deriving from efficient flight behaviours. As juvenile golden eagles are provided with food by their parents, increased feeding behaviour likely reflects high food availability and/or high parental quality. Favourable food conditions during the nestling period are already known to affect later life-stages, including improved fledging body condition (Nebel et al., 2020), shifts in the timing of natal dispersal (Fattebert et al., 2019; Scherler et al., 2023), and increased survival rates (Perrig et al., 2017). Improved nestling food conditions can also induce physiological changes such as improved immune defence or reduced stress levels (Catitti et al., 2022). Therefore, we suggest that favourable feeding conditions during the post-fledging period provided individuals with similar benefits as favourable feeding conditions during the nestling period. However, as food conditions in the nestling period and in the post-fledging period are most likely highly correlated within the same territory and with the same parents, the effect of feeding on the timing of natal dispersal most probably represents the total effect of early-life food conditions, rather than only the effect of post-fledging food conditions.

(d) Conclusions and future directions

The results of this study indicate that juveniles experiencing favourable post-fledging conditions can maximise energy intake and minimise energy expenditure. This likely promotes a faster maturation compared to their peers developing under poor environmental conditions. Favourable food resources (energy intake) and favourable energy resources in terms of environmental uplifts (energy expenditure) show separate advancing effects on the timing of natal dispersal. Early emigration could have subsequent benefits such as improved information gathering or competitive advantages (Clobert et al., 2012). We thus suggest that both food availability and uplift availability in the parental territory translate into long-term positive fitness consequences in juvenile golden eagles.

Late emigration might not only be indicative of poor physical conditions and low flight efficiency, associated with poor future performance, but might also affect the next reproductive cycle of the parents due to a potential trade-off between a prolonged investment into the current offspring and the investment into the next breeding attempt (Grüebler & Naef-Daenzer, 2008; Jenny et al., 2024). Our results suggest that the parental territory drives post-fledging behaviours and emigration decisions. By occupying territories with high-quality food resources and high-quality energy landscapes, parents may have both high-quality offspring and a considerably higher lifetime reproductive success than pairs occupying low-quality habitats.

3.6 Supporting information

Acknowledgments

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Declaration of originality

We declare we came up with the research question, conducted the analysis and wrote the full text ourselves. We used PerplexityAI for the purpose of correcting grammatical and punctuation mistakes in our text using the statement: “Correct grammatical, spelling and punctuation mistakes in the following text without any alteration of the content”.

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Ethics statement

Catching, ringing and tagging were conducted under the licences of the responsible institutions in the different countries and disturbance was kept to a minimum (CH: Food Safety and Veterinary Office Grisons, permit no. GR 2017_06, GR 2018_05E, GR 2019_03E, GR/08/2021, and the Federal Office for the Environment, licence no. TV201903E; DE: birds were handled, tagged and ringed under the permission issued by the government of Oberbayern (2532.Vet_02-16-88 and 2532.Vet_02-20-86); IT: the permissions for handling, tagging and marking were obtained from autonomous region of South Tyrol (Dekret 12257/2018 and Dekret 8788/2020), as well as from the Regione Lombardia and Sondrio Province for ringing and tagging in Lombardia and South Tyrol by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale) with the Richiesta di autorizzazione alla cattura di fauna selvatica per scopi scientifici (l.r. 26/93); AT: permission for handling and tagging falconry golden eagles was issued by the Federal Ministry of Education, Science and Research of Austria, Nr.: GZ 2020-0.369.719).

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3.8 Supplementary material

Table S1. Features extracted from each tri-axial accelerometer bursts (7.9 seconds). Raw ACC values were first transformed into gravitational force g using the function TransformRawACC of the package ‘moveACC’ version 0.1 (Scharf, 2021). We extracted the variance explained by the first thee principal components, ‘ODBA, ‘amplitude’, ‘FFT’, ‘Eigenvalue’, ‘Variance dominant wave’, and ‘Variance remaining’ using the function ‘waveACC’ (Scharf, 2021). ‘Skewness’ and ‘kurtosis’ were calculated using the package ‘moments’ version 0.14 (Komsta & Novomestky, 2022)

Feature	Label	Description	Reference
Features calculated per axis			
Static acceleration	burstmeanx, burstmeany, burstmeanz	Burst mean represents static acceleration from which body posture in each axis can be derived	(Bom et al., 2014; Hounslow et al., 2019; Nathan et al., 2012; Shamoun-Baranes et al., 2012)
Dynamic acceleration	dynxmean, dynymean, dynzmean	Burst mean of the acceleration after subtracting the static acceleration representing movement in each axis	(Bom et al., 2014; Hounslow et al., 2019; Yoda et al., 2001)
Standard deviation	sdx, sdy, sdz, dynxsd, dynysd, dynzsd	Standard deviation for the static and dynamic acceleration per axis	(Bom et al., 2014; Hounslow et al., 2019; Nathan et al., 2012; Shamoun-Baranes et al., 2012)
Skewness	skewx, skewy, skewz	Measure of asymmetry about mean for static and dynamic acceleration in each axis	(Bom et al., 2014; Hounslow et al., 2019; Nathan et al., 2012; Shamoun-Baranes et al., 2012)
Kurtosis	kurtx, kurty, kurtz	Measure of weight of tailedness relative to normal distribution for static acceleration in each axis	(Bom et al., 2014; Hounslow et al., 2019; Nathan et al., 2012; Shamoun-Baranes et al., 2012)
Minimum	xmin, ymin, zmin, dynxmin, dynymin, dynzmin	Minimum measurement of the static and dynamic acceleration per axis	(Bom et al., 2014; Hounslow et al., 2019; Nathan et al., 2012; Shamoun-Baranes et al., 2012)
Maximum	xmax, ymax, zmax, dynxmax, dynymax, dynzmax	Maximum measurement of static and dynamic acceleration per axis	(Bom et al., 2014; Hounslow et al., 2019; Nathan et al., 2012; Shamoun-Baranes et al., 2012)
Trend	trendx, trendy, trendz	linear regression coefficient per axis	(Bom et al., 2014; Nathan et al., 2012)
Autocorrelation	autcorxmean, autcorymean, autcorzmean, autcorxsd, autcorysd, autcorzsd	Mean and standard deviation of the autocorrelation per axis	(Brown, Kays, Wikelski, Wilson, & Klimley, 2013; Nathan et al., 2012)
Pairwise calculated features			
Axes correlation	xycorr, xzcorr, yzcorr	Correlation between two axes	(Brown et al., 2013; Nathan et al., 2012)
Axes crossing	xycross, xzcross, yzcrss	Number of crossings between two axes	(Brown et al., 2013; Nathan et al., 2012)
Features calculated using all three axes			
ODBA	odbaAvg, odbasd	Mean ODBA and standard deviation of ODBA calculated using all three axes	(Bom et al., 2014; Nathan et al., 2012; Scharf, 2021)
Amplitude	amplitude	Amplitude of the calculated FFT wave	(Brown et al., 2013; Scharf, 2021; Yoda et al., 2001)
Fast Furier Transformation FFT	beatsSec	Dominant frequency of the FFT wave	(Scharf, 2021)
Eigenvalue	eigenValue1	Eigenvalue of the wave of PC1	(Scharf, 2021)
Variance dominant wave	varOrigWave	Variance of the wave of PC1 from which the wing beats are extracted.	(Scharf, 2021)
Variance remaining	varRestWaves	Variance of all the waves remaining in the burst after extracting the wing beat wave	(Scharf, 2021)
Roll	rollanimaltrack	Angle between the left-right axis and the horizon	(Shamoun-Baranes et al., 2012; Shepard et al., 2008; Wilson et al., 2006)
Pitch	pitchanimaltrack	Posterior-anterior axis position of an animal	(Shamoun-Baranes et al., 2012; Shepard et al., 2008; Wilson et al., 2006)
Principle component	propExplPC1, propExplPC2, propExplPC3	Proportion explained by each axis of the Principle Component Analysis	(Scharf, 2021)

Table S2. Accuracy measures for the behavioural classification using the random forest applied to the falconry (‘FALCONRY’) and the free-ranging (‘WILD’) golden eagle testing datasets. The numbers next to each behavioural class represent the sample sizes of the behavioural class in the falconry and the free-ranging datasets, respectively. Behavioural class-specific measures as well as the overall model statistics are shown.

Behavioural class	**Sensitivity**		**Specificity**		**Detection rate**		**Balanced accuracy**	
	‘FALCONRY’	**‘WILD’**	**‘FALCONRY’**	**‘WILD’**	**‘FALCONRY’**	**‘WILD’**	**‘FALCONRY’**	**‘WILD**
Feeding (40|8)	1	1	0.99	0.94	0.19	0.04	0.95	0.97
Flapping (40|25)	0.9	0.92	0.98	1	0.18	0.13	0.93	0.96
Soaring (40|53)	0.93	0.96	0.98	0.99	0.21	0.28	0.95	0.98
Roosting (40|76)	0.88	0.87	0.98	0.99	0.18	0.36	0.93	0.92
Undulating (4|1)	0.75	0	1	1	0.02	0	0.88	0.5
Preening (28|15)	0.89	0.53	0.99	0.98	0.13	0.04	0.94	0.75
Walking (8|3)	1	0.67	0.99	0.97	0.04	0.01	1	0.82
Overall statistics								
Accuracy	0.92 / 0.87							
95 % CI	0.87 – 0.95 / 0.82 – 0.92							
Kappa	0.90 / 0.83							

Table S3. Confusion matrix contrasting the observed vs predicted behavioural classes of the falconry ('FALCONRY') and free-ranging golden eagle ('WILD') validation datasets. The number of correctly classified behaviours is shown in bold.

Behaviour	**Data set**	**Feeding**	**Flapping**	**Soaring**	**Roosting**	**Undulating**	**Preening**	**Walking**	**Total predicted**
Feeding	'FALCONRY'	**40**	0	0	2	0	0	0	42
	'WILD'	**8**	1	2	5	0	2	1	19
Flapping	'FALCONRY'	0	**36**	3	0	1	0	0	40
	'WILD'	0	**23**	0	0	0	0	0	23
Soaring	'FALCONRY'	0	4	**37**	0	0	0	0	41
	'WILD'	0	0	**51**	0	1	0	0	52
Roosting	'FALCON'	0	0	0	**35**	0	3	0	38
	'WILD'	0	0	0	**66**	0	1	0	67
Undulating	'FALCONRY'	0	0	0	0	**3**	0	0	3
	'WILD'	0	0	0	0	**0**	0	0	0
Preening	'FALCONRY'	0	0	0	2	0	**25**	0	27
	'WILD'	0	0	0	4	0	**8**	0	12
Walking	'FALCONRY'	0	0	0	1	0	0	**8**	9
	'WILD'	0	1	0	1	0	4	**2**	8
Total observed		48	65	93	116	5	43	11	381

Table S4. Model estimates of the Bayesian multinomial mixed-effects model investigating the effects of the linear and quadratic term of days after fledging, as well as sex on the probability for each behaviour and random effect. Roosting is set as the reference category. Shown are posterior means (estimate), 95% credible intervals (95% CrI) and posterior probabilities (PP) of parameter estimates. Effects with CrI excluding zero and a PP ≥ 0.95 are shown in bold and effects with a PP ≥ 0.90 and < 0.95 in italics.

		Estimate	95% CrI	PP (> or < 0)
Intercept	Feeding	**-2.10**	**-2.21 to -1.98**	**1.00**
	Flapping	**-4.17**	**-4.39 to -3-94**	**1.00**
	Soaring	**-3.59**	**-3.89 to -3.27**	**1.00**
	Undulating	**-7.22**	**-7.68 to -6.77**	**1.00**
	Preening	**-1.98**	**-2.20 to -1.78**	**1.00**
	Walking	**-3.57**	**-3.74 to -3.40**	**1.00**
Linear effect day after fledging	Feeding	0.49	-1.64 to 2.68	0.67
	Flapping	**21.05**	**17.04 to 24.7**	**1.00**
	Soaring	**27.52**	**20.67 to 33.23**	**1.00**
	Undulating	**18.48**	**12.63 to 24.24**	**1.00**
	Preening	**-2.45**	**-4.16 to -0.76**	**1.00**
	Walking	**-2.29**	**-4.60 to -0.00**	**0.98**
Quadratic effect day after fledging	Feeding	**-1.62**	**-2.65 to -0.58**	**1.00**
	Flapping	**-4.12**	**-6.01 to -2.26**	**1.00**
	Soaring	**-4.40**	**-6.55 to -2.27**	**1.00**
	Undulating	-2.15	-6.98 to 2.58	0.81
	Preening	0.18	-0.55 to 0.93	0.69
	Walking	**1.97**	**0.60 to 3.32**	**1.00**
Sex (male)	Feeding	0.01	-0.11 to 0.14	0.57
	Flapping	*0.23*	*-0.10 to 0.56*	*0.92*
	Soaring	0.14	-0.21 to 0.50	0.78
	Undulating	**0.71**	**0.14 to 1.28**	**0.99**
	Preening	**0.35**	**0.06 to 0.66**	**0.99**
	Walking	0.13	-0.10 to 0.38	0.86
Sd Date (220)	Feeding	0.48	0.43 to 0.55	
	Flapping	0.30	0.24 to 0.37	
	Soaring	0.73	0.64 to 0.83	
	Undulating	0.63	0.42 to 0.85	
	Preening	0.17	0.15 to 0.21	
	Walking	0.26	0.21 to 0.32	
Sd BirdID (36)	Feeding	0.19	0.14 to 0.26	
	Flapping	0.45	0.34 to 0.59	
	Soaring	0.52	0.40 to 0.69	
	Undulating	0.61	0.40 to 0.89	
	Preening	0.44	0.35 to 0.57	
	Walking	0.31	0.22 to 0.44	
Sd BirdID : Linear effect day after fledging (36)	Feeding	3.85	2.64 to 5.49	
	Flapping	9.11	6.14 to 12.92	
	Soaring	13.75	9.83 to 19.17	
	Undulating	2.55	0.08 to 8.75	
	Preening	3.87	2.84 to 5.22	
	Walking	5.07	3.09 to 7.52	

Table S5. Estimates of the model investigating factors affecting the timing of emigration including the four early emigrating individuals. Shown are parameter means (Estimate), 95% credible intervals (95% CrI) and posterior probabilities (PP) derived from random draws of 14’000 linear mixed-effects models. The models used the posterior draws of the random effects extracted from the multinomial model. Effects with a posterior probability ≥ 0.95 are printed in bold and effects with a PP ≥ 0.90 and < 0.95 in italics.

	Estimate	95% CrI	PP (> or < 0)
Intercept	**180.31**	**149.00 to 212.15**	**1.00**
Time spent flapping	17.69	-11.65 to 48.01	0.88
Increase of flapping	14.91	-12.22 to 41.21	0.87
Time spent soaring	*-20.99*	*-49.65 to 8.57*	*0.92*
Increase of soaring	4.34	-20.70 to 28.86	0.64
Food intake time	**-26.00**	**-47.34 to -3.55**	**0.99**
Sex (male)	16.06	-34.85 to 65.42	0.74

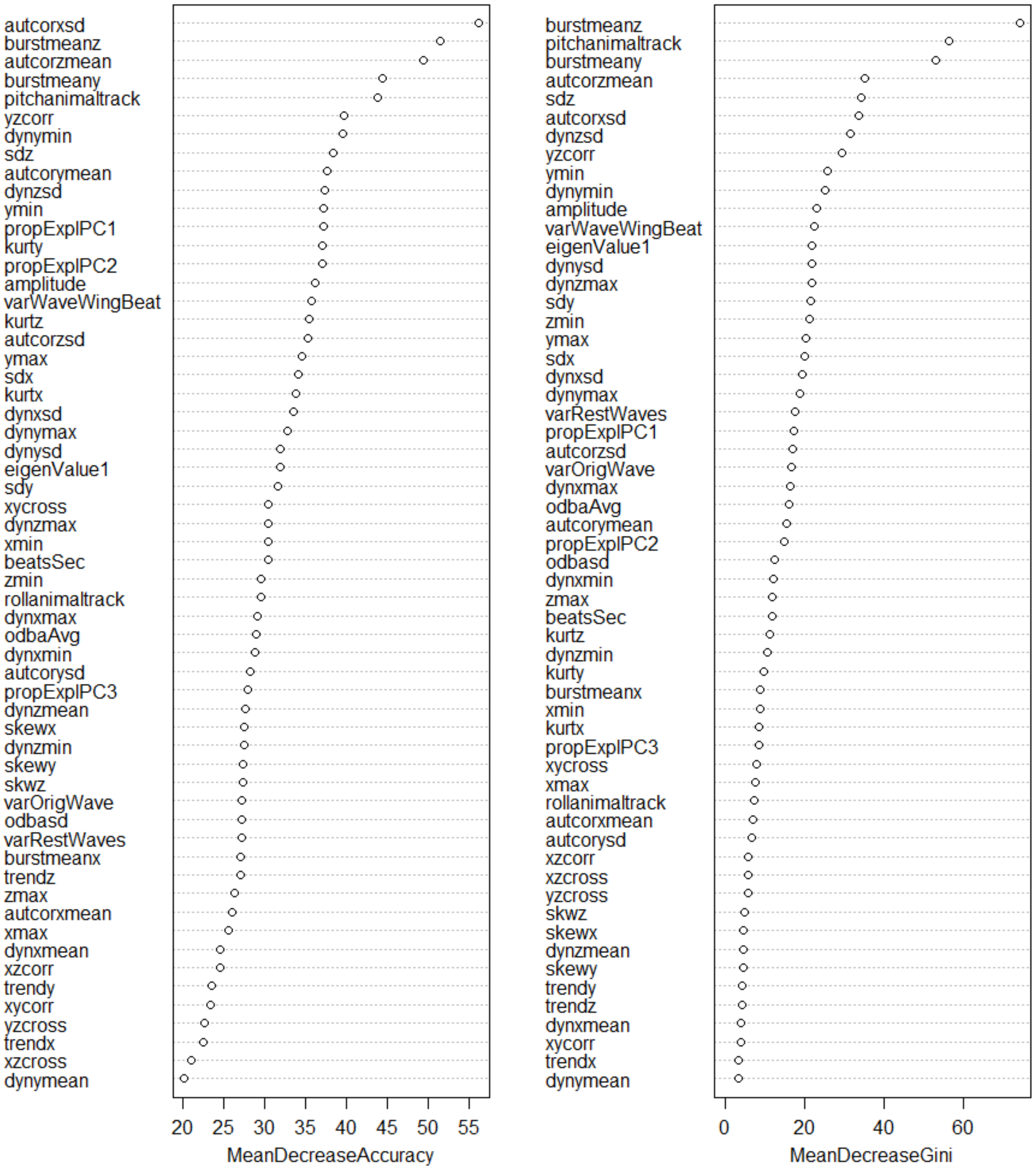

Figure S1: Variable importance of the predictor variables used in the random forest classifications for identifying golden eagle behaviours. Represented is the mean decrease in accuracy and mean decrease in the Gini Index for each variable. Higher values of mean decrease indicate variables that are more important for the classification. Variable descriptions are given in Table S1.

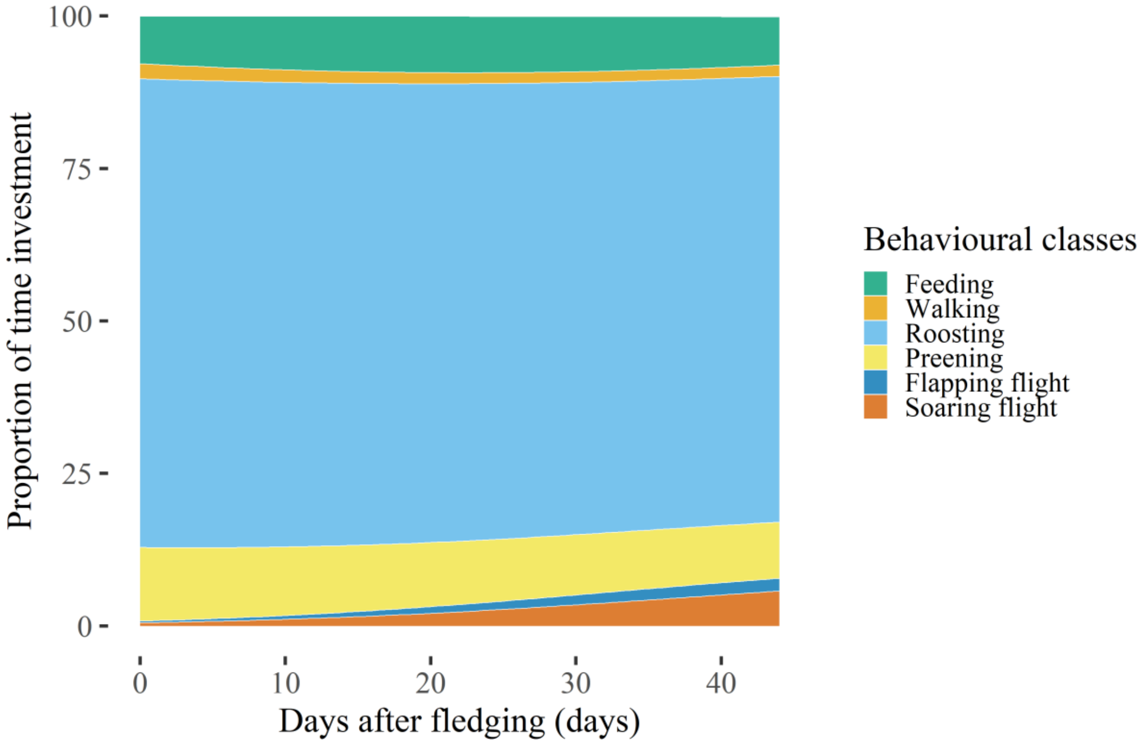

Figure S2. Time budget of juvenile golden eagles in relation to the time after fledging in days. Model predictions for females of the mean proportion of time invested in each behaviour are shown. Note that all behaviours add up to 100% of the total available time between 4:00 – 17:00 UTC. Undulating flight is missing from the plot as it contributed to less than 1% of the time budget.

4. Chapter III

Rearing conditions determine movement behaviours in a large raptor during natal dispersal

Julia S. Hatzl [a, b], Kamran Safi [c], Enrico Bassi [d, e], David Jenny [a], Matthias Tschumi [a],
Martin U. Grüebler [a]

Illustration: Lara Gross

Affiliations

[a] Swiss Ornithological Institute, Sempach, Switzerland.

[b] Department of Landscape Ecology, ETH Zürich, Zürich, Switzerland
[c] Department of Migration, Max Planck Institute for Animal Behaviour, Radolfzell, Germany
[d] Vulture Conservation Foundation Advisory Board, Zürich, Switzerland.
[e] Italian Ornithological Studies Center CISO

E-mail addresses and ORCIDs of co-authors:

J. S. Hatzl: julia.hatzl@vogelwarte.ch; ORCID**: 0000-0002-7915-9588**
K. Safi: ksafi@ab.mpg.de; ORCID: 0000-0002-8418-6759
E. Bassi: enrico.bassi76@gmail.com; ORCID: 0000-0002-0698-4800
D. Jenny: jenny.d@compunet.ch, ORCID: 0000-0003-3027-0004
M. Tschumi: matthias.tschumi@vogelwarte.ch; ORCID: 0000-0002-7991-7780
M. U. Grüebler: martin.gruebler@vogelwarte.ch; ORCID: 0000-0003-4468-8292

Keywords

Natal dispersal, carry-over effects, transience, early-life effects, soaring raptor, movement behaviour

Chapter notes

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Authors contributions

J.S.H., M.U.G., K.S conceived the idea. J.S.H., K.S., D.J., E.B. carried out the fieldwork. J.S.H. conducted the formal analysis. Methodology was developed by J.S.H., M.U. G., M.T., K.S., D.J.; J.S.H. wrote the first draft of the manuscript and all authors contributed substantially to the revisions.

4.1 Abstract

Animal movement and space use are shaped by resource distribution and availability, influenced by an animal's intrinsic drive to access these resources. Individuals differ in their ability to access resources, and one important factor underlying this difference are the conditions that they experienced during early life. Favourable early-life conditions can enhance resource access, reducing the need to move to new habitat patches, especially in high competition scenarios. Here we examine how early-life conditions and increasing experience impact the movement behaviour of juvenile Alpine golden eagles during transience—the period between leaving the natal territory and first reproduction. In this population, better conditions at natal site relate to earlier emigration from the parental territory. We expected that with increasing age individuals can make more informed decisions, thereby reducing costs of movements individuals growing up under better conditions relocate less due to higher competitiveness compared to their peers. Contrary to our expectations, though, we found that the intensity of area use decreased with time spent in transience, indicating increased movement as juveniles aged. This change was primarily driven by early emigrating individuals growing up under favourable conditions. Increased mobility in these individuals was linked to prolonged exploration behaviour and reduced encampment. Our findings contrast with previous studies on transience in other species, likely due to the conditions prevailing in dense populations. Early emigrating individuals might be more competitive, better in flying capabilities or mature more rapidly, aiding in navigating a competitive landscape. This study provides insights into how early-life conditions affect individual fitness and population dynamics, potentially influencing successful recruitment into the breeding population.

4.2 Introduction

The way animals move and use space is driven by the distribution and availability of vital resources (Charnov, 1976b; Lendrum, Anderson, et al., 2014). Such vital resources include food (Fryxell et al., 2004; Lamb et al., 2017; Müller et al., 2023), breeding sites, environmental conditions facilitating movement corridors or wind support (Kouba et al., 2017; Nourani & Yamaguchi, 2017; Sur et al., 2019), as well as a favourable social environment (Laundré et al., 2001; Lendrum, Elbroch, et al., 2014). In areas of low resource availability animals travel longer distances and therefore the area they use to meet their demands usually expands (Kouba et al., 2017; McIntyre & Wiens, 1999). In contrast, when resources are abundant, space use and movement extent are reduced accordingly (Kareiva & Odell, 1987). Animal movement can thus be viewed as an expression of external factors acting on the animals in their pursuit of key resources. It is through their movements that animals optimise their use of habitat patches to ultimately gain fitness benefits (Charnov, 1976a; Mohlenhoff et al., 2017; Morris & Davidson, 2000).

Since the way animals move and use space tightly reflects the availability and utilisation of resources, changes in movement are reminiscent of spatial and temporal variation of resource availability. The variable resource availability interacts with intrinsic factors of individuals, scaling up to population and species-level movement patterns. Body condition (Rémy et al., 2011), life-history stage (Del Mar Delgado et al., 2009; Lubitz et al., 2022) or sex (Barbraud et al., 2003; Sur et al., 2019) are just a few of the factors that can affect the use of resources causing differential movement patterns in otherwise similar environments (Nathan et al., 2008). Multiple external and internal factors can interact to invoke a complex interplay shaping resource use and thus movement. Elephants, for instance, segregate spatially according to the social dominance rank of the group during resource poor seasons, whereas during resource rich seasons such socially heterogeneous groups occur within the same areas (Wittemyer et al., 2007). This highlights how the availability and use of resources mediated through movement processes operate along all scales to drive the segregation or aggregation of individuals (Aarts et al., 2021; Catitti et al., 2024; Wittemyer et al., 2007), populations (Pinaud & Weimerskirch, 2007; Shigesada et al., 1979), and even affect species diversification (Jousset et al., 2016; Kokko & López-Sepulcre, 2006; Levis et al., 2017).

Early-life conditions have a strong potential to modify individual behaviours and movement patterns at later life stages (Catitti et al., 2024; Lindström, 1999; Metcalfe et al., 2014) and can even influence reproductive output (Burton & Metcalfe, 2014; Sloboda et al., 2011; Sorensen et al., 2022) and adult survival (Catitti et al., 2024; Elo & Preston, 1992). Multiple species show pervasive fitness benefits resulting from favourable conditions experienced during early life (referred to as the silver spoon hypothesis (Stamps, 2006; Van De Pol & Verhulst, 2006). The consequences of early-life conditions on resource use and movement patterns are hardly documented in long-lived species within their natural habitats due to the difficulties in acquiring data across life-history stages. This begs the question as to how the known fundamental consequences attributed to different early-life conditions alter the interplay of external and internal factors throughout different life-history stages.

A key life-history stage in many species is the transience (wandering) phase that marks the onset of independence from parental care. During transience individuals move through the landscape matrix, acquiring knowledge and experience before settling for their first reproduction (Clobert et al., 2004). With the progression of transience, individuals accumulate knowledge about the resource distribution that allows them to make informed movement decisions about where and for how long to remain stationary, and eventually where to settle (Piper et al., 2015). It has been shown that with approaching sexual maturity, individuals increasingly resemble adults in their movement behaviour, spending more targeted and prolonged periods in suitable habitats and gradually becoming sedentary (Delgado et al., 2009). During transience, individual survival is often low because of the high costs associated with moving through unknown terrain in contrast to the natal or settlement phases (Bowler & Benton, 2005). Early-life conditions could thus have cascading effects throughout the transience period, giving rise to differential movement and resource use patterns (Catitti et al., 2024; Fattebert et al., 2019; Rémy et al., 2011; Van De Pol & Verhulst, 2006).

Alpine golden eagles are particularly suited to investigate long-time carry-over effects because they are long-lived soaring birds that experience prolonged parental dependency. The extended subsequent transience phase (Haller, 1996) provides the grounds for early-life conditions to act and manifest. Indeed, we have recently documented the impacts of the first weeks in the life of golden eagles on the timing of independence from parental care (Chapters I and II; Zimmermann, 2021). Juvenile golden eagles experience different early-life advantages by fledging earlier, developing energy-efficient soaring skills sooner, growing up under more favourable food conditions, and by undertaking foray flights outside the natal territory more often than their peers. All these correlates of favourable early-life conditions in the Alpine golden eagles manifest as accelerated development and earlier independence from parental care by emigrating sooner from their natal territories (Chapters I and II; Zimmermann, 2021). The benefits gained in early life might consequently help later to negotiate the highly competitive environment these birds will have to navigate once emigrated. The territorial Alpine population of golden eagle is considered to have reached carrying capacity (Haller, 1996; Jenny et al., 2024; Jenny, 1992) where resources for transient individuals are strongly limited. There, limitation of resources and space likely fuels competition among conspecific juveniles but also leads to deadly agonistic encounters between juveniles and territorial golden eagles (Jenny et al., 2024).

Due to the fierce competition, we expect resource availability and use to be strongly affected by individual competitiveness. To investigate this, we quantified how the movement of juvenile Alpine golden eagles developed over the course of transience, and the extent to which timing of emigration, a proxy for early-life conditions, affected movement development. Specifically, we characterised space use by (1) the intensity with which juveniles use areas, (2) the duration of two distinct movement behaviours, namely, encampment (i.e. remaining stationary) and exploration (i.e. fast, directed movement). As the eagles age during transience, their competitive disadvantage relative to territorial breeding pairs should level out while simultaneously their advantage towards younger transient individuals should accentuate. This should allow transient individuals to increasingly defend beneficial areas, and we thus expect golden eagles to become increasingly sedentary with age. Further, we anticipate that individuals that emigrated early from their natal habitat have increased access to resources compared to late-emigrating conspecifics of the same age. This advantage should manifest as more pronounced search behaviour and longer encampment. We also expect that the process of reaching adult-like movement behaviour to be accelerated in individuals emigrating early. Hence, we expected a more rapid transition towards more sedentary movement and longer encampment durations with age.

4.3 Methods

Study species and study area

Golden eagles occur throughout the northern hemisphere but within central Europe they are mainly restricted to the mountainous and alpine habitats. The Alpine golden eagle population is non-migratory, despite the high seasonality of the Alpine region and the vast amounts of snow in winter months. Established breeding pairs uphold territorial boundaries throughout the year that are defended aggressively against conspecifics (Haller, 1996; Jenny et al., 2024). The strong topographical relief enables orographic and thermal energy build-up, which golden eagles require for subsidising flight costs (Duriez et al., 2014). Low anthropogenic development, large numbers of herbivores and stringent protection have resulted in a high density of 1.4 golden eagle pairs/100 km^2 in the Central Alps (Jenny et al., 2024).

Juvenile golden eagles remain within their natal territory for about ten months after hatching (Haller, 1996; Weston et al., 2013; Zimmermann, 2021). Once emigrated permanently from their natal home range, juveniles are transient for multiple years during which they move through the landscape without occupying a territory (Haller, 1996; Watson, 2010). The transience period usually ends with the establishment of a territory followed by a first reproduction (Clobert et al., 2012). However, in golden eagles the transience period is often prolonged and can last well beyond the four years which is typically required for individuals to reach sexual maturity (Jenny et al., 2024; Watson, 2010). Especially in areas with high golden eagle densities, the transience period can be extended to seven years or more (Haller, 1996; Jenny et al., 2024), whereas in areas with lower population densities golden eagles show territorial behaviour already at an age of two (Whitfield et al., 2022). Juvenile golden eagles are highly dependent on (ungulate) carrion throughout their first years of transience, but they gradually transition to an active hunting strategy. In contrast, mainly rely on carrion during winter whereas during summer they predominantly hunt (Jenny et al., 2024). This results in a seasonal dietary difference between adults and juveniles with juveniles mainly feeding on ungulate carcasses year-round and adults preying on marmots (M*armota marmota*), grouse species (*Tetraoninae*) as well as juvenile chamois (R*upricapra ruupricapra*) and ibex (*Capra ibex*) during summer (Haller, 1996).

Collection of movement data

We collected Global Positioning System GPS location data by deploying solar powered GPS tags (e-obs reference) on 48 juvenile golden eagles during 2017 – 2022 (2017: 2, 2018: 5, 2019: 19, 2020: 9, 2021: 7, 2022: 6). We deployed solar powered GPS tags to 50 day old nestlings (±3 days)). We attached the tags with a leg-loop harness to minimize the impact of device attachment on flight performance and to allow the unrestricted development of the pectoral muscles—a muscle which mainly develops after fledging (Longarini et al., 2023). Combined tag and harness weight did not exceed 60 g, which is well below the recommended threshold of 3% of an individual's body weight (Kenward, 2001). For details on deployment and data collection please refer to Chapter I and I.

Location data were automatically transmitted and stored in the online repository movebank.org (Wikelski et al., 2022), from where we downloaded data using the 'move' package version 4.1.12 (Kranstauber et al., 2023). All analyses and data processing were done using the software R version 4.2.1 (R Core Team, 2020). To retain the data of the transience period, we filtered the location data for each individual to include only the period between emigration (defined using a distance-threshold method (Weston et al., 2013; Zimmermann, 2021)) and the dedicated endpoint of the study period (i.e. June 29th, 2023). For some individuals, data transmission stopped before the end of the study period due to death (n = 5), suspected settlement without reproduction (n = 1), logger failure (n = 14), or tag loss (n = 6). Tags recorded locations once an hour (06:00 – 19:00 UTC in April – November; 09:00 - inter and additional high-resolution data every second during periods of high battery charging (Chapter II). Occasional data gaps and irregular recording of locations could occur due to insufficient recharging of the solar-powered battery. As we were interested in area use intensity on a multiday scale, we applied velocity filtering to reduce spatial noise and retained only the first and last location per day. Reducing the spatial noise was suggested to result in a clearer picture of changes in space use (Vincent et al., 2002). In cases where the first and last location of a day were less than six hours apart from one another, we retained only one location. To reduce the effect of data gaps we split the movement trajectory into individual segments when no location data was collected for more than two days consecutively using the package 'adehabitatLT' version 0.3.26 (Calenge, 2006). Furthermore, we excluded segments shorter than 10 days. This resulted in a total of 122 trajectory segments used for further analysis of the movement process.

Determining the movement process and space-use intensity

To describe the processes underlying the observed movement trajectory, we derived first passage time (FPT). FPT quantifies the time needed to leave a circle of a predefined radius at each location along a trajectory- and therefore is a measure for space-use intensity (Johnson et al., 1992). Large FPT values indicate periods where individuals intensively used an area, displaying undirected random or even subdiffusive movement for a long period of time. Low FPT values are associated with more directed movement and hence shorter-term and less intensive use of an area. Using FPT allowed us to integrate information on both speed and turning angle into one measurement to describe the movement process. FPT is highly connected to turning angles and speed as high values of FPT are associated with high turning angles and low speed and low FPT values with low turning angles and high speed (Pinaud, 2008).

Similar to other models assessing movement processes, the FPT analysis is scale dependent. As movement processes happen at different spatial scales, the spatial scale at which individuals show an increase of area use intensity, e.g. the radius, needs to be chosen according to the biology of the species and the research question. We chose the radius according to the first explicit local maxima identified by the analysis of the relative variance of the log-transformed FPT values (Byrne & Chamberlain, 2012; Fauchald & Tveraa, 2003). We tested values along increasing radii from 500 m – 15’000 m in increments of 100 m and identified the first local maxima at a radius of 3’900 m (figure S1). We reran the following analysis with radii corresponding to further local maxima at 2’600 m, 5’000 m and 6’700 m and obtained comparable results (table S1).

Modelling the movement process: First Passage Time (FPT)

To understand how the movement process evolves and how it is affected by early-life conditions, we fitted a generalised linear mixed-effects model (GLMM) modelling FPT as a function of the emigration timing, age, sex and season as fixed effects. We used the emigration timing (period between tagging until emigration from the natal territory) as a proxy for early-life conditions, as early emigration timing showed to correlate with higher activity and favourable food conditions (Chapters I and II; Zimmermann, 2021). To assess possible amplifying effects of early-life conditions with, we incorporated an interactive term between emigration timing and age. Age refers to the number of years since the 31st of September of the year of emigration. Including a variable for summer (1. May – 31. September) and winter (1. October – 31. April) allowed us to account for seasonal variability in the movement process. Sex was genetically determined using blood quills collected during the tagging. To assess population-level effects irrespective of individual and habitat differences we included individual ID (n = 48), territory ID (n = 39) and the year of birth (n = 6) as well as the date (n = 1'941) as random effects. We used a nested structure for individual and territory as several individuals were tagged within the same territory. An additional random effect for the date the location was collected allowed us to account for similar environmental conditions. All continuous predictor variables were z-transformed to facilitate model convergence and to allow comparability of model coefficients. We found no relevant autocorrelation between any numeric explanatory variable (all pearson's $r < |0.07|$).

The distribution of FPT was skewed and deviated from a Gaussian distribution. To meet statistical assumptions of the model, we applied a log transformation of FPT to achieve a normal distribution of the residuals. Introducing an autocorrelation term of structure type 1 into our model allowed us to account for existing temporal autocorrelation but no spatial autocorrelation was detected. We defined the structure of our models based on biological hypotheses and did not apply any model selection (Korner-Nievergelt et al., 2015). We fitted the statistical model in a Bayesian framework using the package 'brms' version 2.18.0 (Bürkner, 2021) running four Markov chains of 5'000 iterations each, of which we discarded 2'000 as burn-in and retained every second iteration. As recommended by (Gelman, 2006), we used weakly informative, normally distributed priors (mean = 0, sd = 3) for population level effects and adapted delta to 0.99 to decrease the number of divergent transitions.

Encampment and exploration

While FPT is a valuable metric for understanding space use and movement dynamics, segmenting a movement path into distinct movement modes provides a more detailed, and contextually meaningful understanding of animal movement and behaviour (Delgado & Penteriani, 2008). On top of information on the time an individual spends in a specific area, segmentation provides context to this metric by showing fine-scale movement patterns like the duration and change rate between behaviours and the overall time investment into movement behaviours. We therefore classified the movement trajectory into two distinctive movement behaviours—encampment (area restricted search behaviour) and exploration (fast, directed traversing behaviour)—according to the similarity in the use intensity derived from FPT. To identify breakpoints within the movement process where tortuous movement changes to more directed movement we applied Lavielle segmentation (Lavielle, 1998). We determined that an encampment had to last a minimum of three days in which an individual remains within a 3’900 meter radius. The individual movement trajectories were of varying duration, and we had no *a priori* information of how many behavioural segments might exist. Hence, we decided on the highest number of breakpoints possible for each trajectory which likely resulted in an overestimation of breakpoints. Visual inspection of the identified breakpoints indicated an overestimation for which we corrected for by merging movement behaviour units with a similar mean FPT value (mean FPT value of unit > 3 = encampment mean FPT value of unit < 3 = exploration). We conducted both FPT calculation and behavioural segmentation using the package ‘adhabitatLT’ version 0.3.26 with the corresponding functions ‘FPT’ and ‘lavielle’ (Calenge, 2006).

Calculating the duration of encampment and exploration units allowed us to determine whether the duration of each behavioural unit was also affected by early-life conditions and age, and not only the underlying movement process. We thus determined the length of each behavioural unit in days. The first and last behavioural unit per trajectory had to be excluded as we lacked information on the exact start or end point of the unit. We fitted the two statistical models in a Bayesian framework for each movement behaviour separately and used the same fixed effects and interaction term as for the movement process model. As random effects we incorporated individual ID (n = 48), territory ID (n = 39) and year of tagging (n = 6) here. Applying an inverse transformation of the encampment durations and a log-transformation of the exploration durations allowed us to meet the statistical assumption of a normal distribution of the residuals. For both models we ran for chains with 15’000 iterations each and discarded 4’000 iterations of each chain as burn-in. We used the default, normally distributed, weakly informative priors (mean = 0, sd = 3).

All models were checked for convergence of the Markov chains with Brooks-Rubin-Gelman diagnostics (Brooks & Gelman, 1998) and for validity using posterior predictive checks. For all models we calculated posterior probabilities (PP) for model estimates, indicating the probability of the estimates to differ from zero. We considered estimates to have a strong effect if $PP \geq 0.95$ and a weak effect if $0.95 > PP > 0.9$. To aid the interpretation of early-life conditions, age, sex and season, we predicted new values using the model coefficients and derived mean and 95% credible intervals for each fixed effect, while holding all other coefficients constant (Koster & McElreath, 2017). Back-transformation of the predicted residence times allowed for better interpretation in the figures.

4.4 Results

In total, we collected 226’889 days of data from 48 juvenile golden eagles (mean: 558 ± 410 days; range: 7 - 1243 days) across the Alpine range (figure 1a).

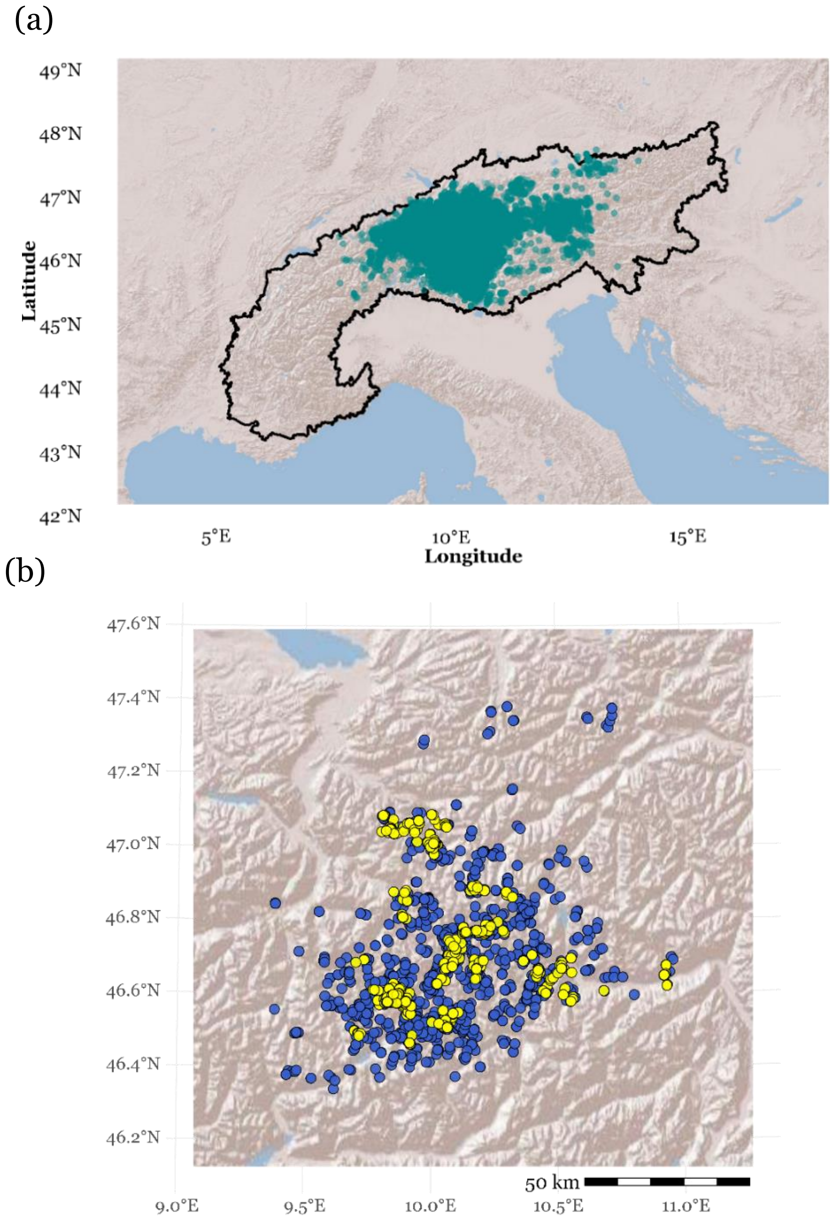

Figure 1. (a) Map of juvenile golden eagle locations included in this study. Green dots represent GPS locations of different birds and the black contour represents the edge of the Alpine range. (b) Map of locations used during encampment (yellow) and during exploration (blue) units of the movement trajectory of one selected individual. The background map indicates the relief of the surface area with darker area representing higher relief and blue indicates water (basemap: Esri World Shaded Relief.; Alpine perimeter: Permanent Secretariat of the Alpine Convention).

All individuals (28 males and 20 females) emigrated from the natal territory between November of the year of hatching and April in the following spring after a post-fledging dependency period of 227 ± 42 days (range: 132 – 285 days). The number of trajectory segments from which we derived First Passage Time (FPT) during transience varied between 1 and 204 days per individual (mean: 72 ± 57 days). Individuals remained within the 3’900 m radius for between 0 and 42 days (mean: 3 ± 4 days) and covered a mean of 11’260 m ± 14’235 m per day (range: 1 – 201’748 m). After segmentation of the tracks, 7’699 locations were classified as encampment and 19’105 locations as exploration (see figure 1b for an example of one selected individual). Encampment units lasted on average 7 ± 6 days (range: 3 – 71 days), whereas exploration units lasted on average 17 ± 18 days (range: 3 – 141 days).

Movement process FPT

We found strong support for an interactive effect of age and emigration timing on FPT (table 1; figure 2). Thereby, the movement process remained largely constant in individuals emigrating late, but movement became faster and more directed with increasing age in individuals emigrating early. Individuals emigrating early decreased FPT by almost a day within the first four years after emigration.

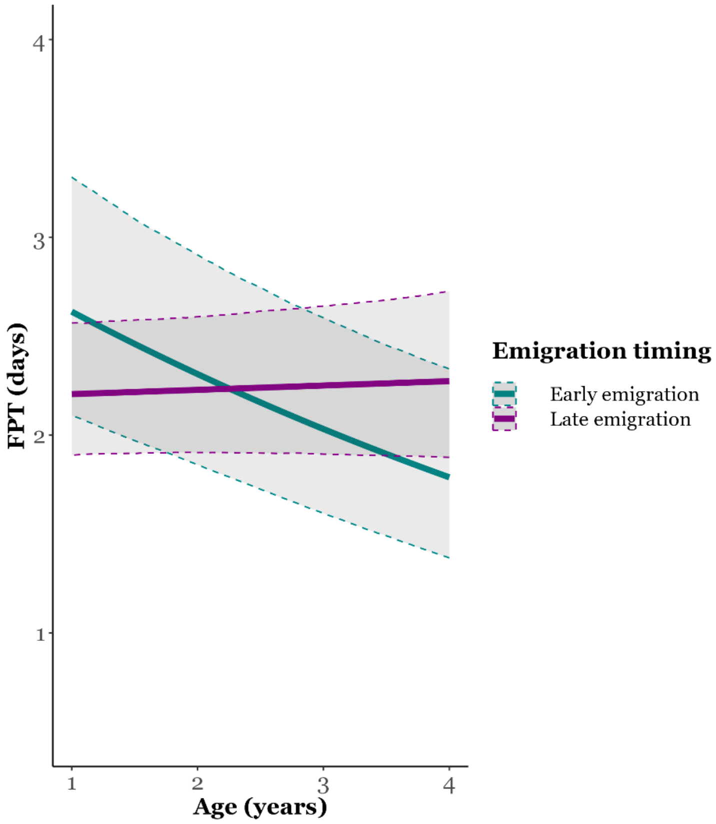

Figure 2. First Passage Time FPT of juvenile golden eagles in relation to individual age and timing of emigration. High FPT values indicate high directedness of a movement path and are a proxy for space-use intensity. Shown is the change in FPT with increasing age for individuals emigrating early (5% quantile; green) and for individuals emigrating late (95% quantile; purple). Solid lines represent the mean values and dotted lines the 95% CrI for females in summer. We back-transformed the predicted FPT values to the original scale to facilitate interpretation.

In their first year, individuals emigrating early had higher FPT than individuals emigrating late but their age-dependent decline in FPT resulted in lower FPT after four years (table 1; figure. 2). In addition, FPT was higher in summer compared to winter and females had higher FPT than males (table 1; figure 2).

Table 1. Parameter estimates of the Bayesian linear mixed-effects models investigating the effects of emigration timing, age, sex, season and the interactions between age and emigration timing on the movement process (First Passage Time; FPT) and the duration of exploration movement units. Parameter means (Estimates), 95% CrI and Bayesian posterior probabilities (PP; i.e. the likelihood for the given effect size to differ from zero) are given. Effects with a posterior probability ≥ 0.95 are printed in bold and are interpreted as having a strong effect. Effects with a posterior probability > 0.90 and < 0.95 are printed in italics and are interpreted as having a weak effect. Model estimates are on the log scale.

	Movement process (FPT)			**Exploration duration**		
Fixed Effects	**Estimates**	**95% CrI**	**PP (< or > 0)**	**Estimates**	**95% CrI**	**PP (< or > 0)**
Intercept	**0.814**	**0.645 to 0.998**	**1.000**	**2.320**	**2.127 to 2.497**	**1.00**
Emigration timing	-0.011	-0.1051 to 0.076	0.602	**-0.065**	**-0.151 to -0.023**	**0.930**
Age	**-0.036**	**-0.065 to -0.008**	**0.993**	0.023	-0.045 to 0.091	0.748
Sex (male)	**-0.136**	**-0.302 to 0.023**	**0.951**	**0.104**	**-0.057 to 0.267**	**0.900**
Season (winter)	**-0.149**	**-0.199 to -0.099**	**1.000**	0.067	-0.048 to 0.181	0.870
Emigration timing x age	**0.040**	**0.013 to 0.066**	**0.998**	*-0.043*	*-0.108 to 0.023*	*0.905*
Territory ID	0.160	0.014 to 0.281		0.135	0.010 to 0.265	
Territory ID : bird ID	0.192	0.098 to 0.293		0.108	0.006 to 0.237	
Year of tagging	0.086	0.003 to 0.292		0.092	0.003 to 0.312	
Date	0.110	0.099 to 0.122				

Duration of encampment and exploration units

Changes in either the number or the duration of movement units can provoke similar patterns in FPT. Therefore, FPT alone does not allow conclusions about movement behaviour persistence or change rate between movement modes. To better understand whether early-life conditions and age effects alter the number or the duration of individual movement units, we modelled the effect of emigration timing, age, sex and season on the duration of discrete movement behaviours—encampment and exploration.

We found support for an interactive effect of age and emigration timing on the duration of exploration units (table 1; figure 3a). Individuals emigrating early undertook longer periods of exploration as they aged, whereas no change was found in individuals emigrating late. Thereby, the increase in exploration units for individuals emigrating early summed to an average of seven days from year 1 to year 4. Accordingly, we found some support for an interactive effect of age and emigration timing on the duration of encampment units (Estimate = -0.005, 95% CrI = -0.011 – 0.001, PP = 0.94; Supporting Information table S2; figure 3b). The duration of encampment units decreased with increasing age for individuals emigrating early, whereas no change was indicated in individuals emigrating late. For individuals emigrating early, the duration of encampment units reduced by an average of two days from year 1 to 4. Overall, males tended to spend longer durations in exploration units than females (table 1) where they did not differ the duration spent in encampment units. Together, these results indicate that both the duration and the frequency of encampment decreased in individuals emigrating early as they got older but remained unchanged in individuals emigrating late.

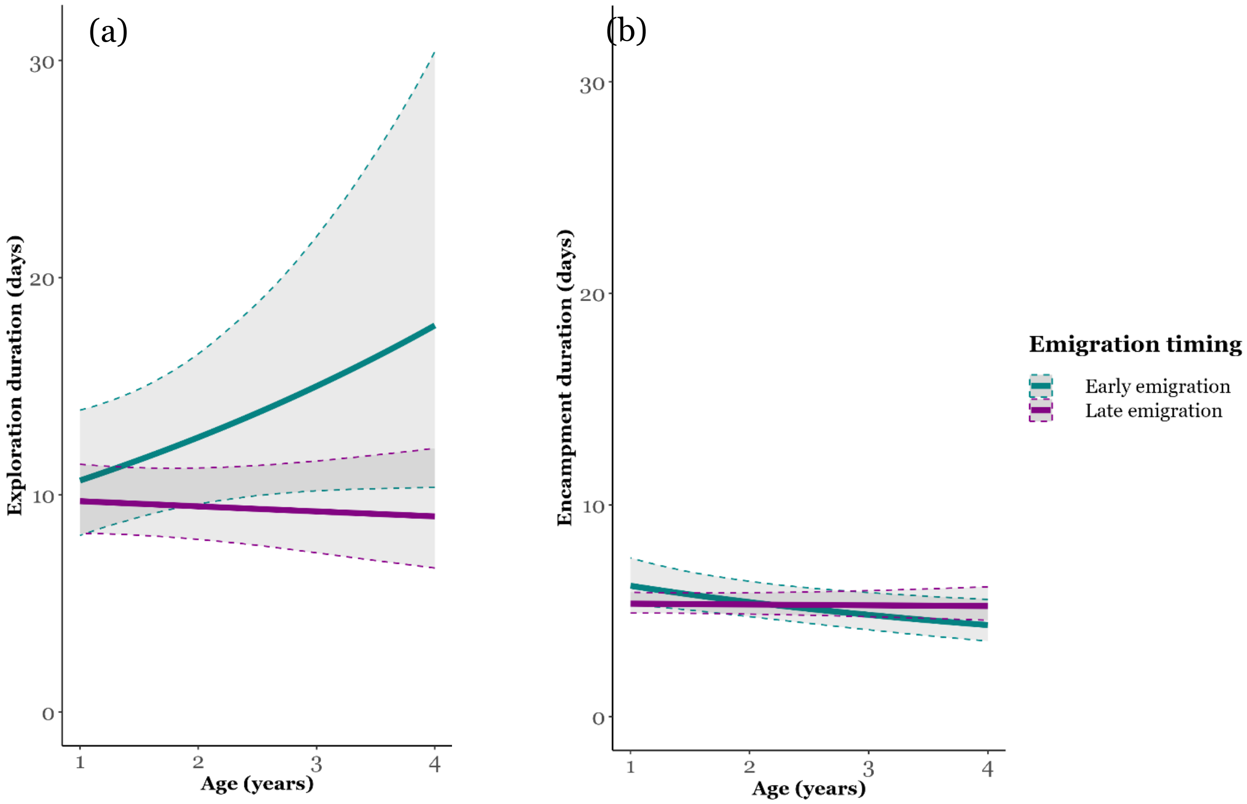

Figure 3. Duration in days spent in (a) exploration and (b) encampment units during the first four years of transience in relation to age and timing of emigration. Shown is the change in days with increasing age for individuals emigrating early (5% quantile; green) and for individuals emigrating late (95% quantile; purple). Solid lines represent the mean values and dotted lines the 95% CrI for females in summer.

4.5 Discussion

Juvenile golden eagles gradually moved more and increased the duration of mobile movement units the longer they spent in transience, contrasting our initial expectations. We found, however, that early-life conditions had fundamental consequences for later-life space use and movement during transience. The increase in movement with age was mainly driven by individuals emigrating early, the cohort that benefits from favourable early-life conditions. Late emigrating individuals did not change their movement behaviour and space use in relation to their age. We argue that the increase in mobility could be induced by juveniles becoming more proficient flyers with age or by a change in the competitive social landscape they have to navigate, and that early-life benefits accelerate maturation processes and increase competitiveness.

Age effect

The higher mobility that we observed as birds aged could have resulted from increased flight efficiency that reduce the cost of movement. Golden eagles, due to their morphology, size, and weight, are highly dependent on externally provided energy for soaring flight. By soaring, they—and many other large soaring birds—can cover large distances while hardly raising energy expenditure above the metabolic baseline (Hedenstrom, 1993). A previous study showed that juvenile golden eagles become more proficient with age in using more challenging thermal uplifts and thus become less dependent on topographical features (Nourani et al., 2024). By gaining experience, juvenile soaring birds can increase their flight performance (Harel et al., 2016) and vertical hight gain (Reddy et al., 2016) even when wind conditions are challenging which increases travel time (Duerr et al., 2015) and reduces energy requirements (Corbeau et al., 2020). Faster climb rates could be particularly important to overcome social barriers as evoked in a saturated population. If it takes transient golden eagles long to reach heights that allow them to safely cross territories or if they need to cross territories at low elevation, they are easily detected and attacked by territory holders (Collopy & Edwards, 1989; Duerr et al., 2019). The well-developed abilities to use environmental energy effectively, typical for older individuals, might help to negotiate such social barriers avoiding aggressive interactions.

This pattern may be reinforced by the intensified competition juveniles encounter as they mature. Increased mobility in older individuals may therefore also result from heightened territorial interactions. On one hand, agonistic behaviour exhibited shown by territory holders generally increases as juveniles mature (Piper et al., 2022). It has been hypothesised that the distinctive juvenile plumage, characterised by prominent white wing patches and a white tail base, serves as a protective mechanism to conspecific aggression (Gjershaug et al., 2019; Haller, 1996), signalling inferior competitive abilities for breeding sites (Ellis & Lish, 2006). During the four to five years of maturation, the plumage becomes increasingly similar to that of adults (Bloom & Clark, 2001) which could provoke more and more aggressive attacks. On the other hand, the internal motivation to establish territories may also increase as transient individuals mature, potentially driving their motivation to actively engage more frequently in conflict situations. In oystercatchers, territorial intrusion behaviour of maturing individuals has been proposed to benefit information gathering and site familiarisation, which aids in successful territory establishment (Bruinzeel & Van De Pol, 2004). Transient individuals approaching maturity are thus likely to increasingly explore potential territories with the aim to establish a territory, find a mate, which results in a behavioural change (Goodall, 1986). In a densely populated environment, frequent competitive interactions can significantly elevate the energetic demands on both transient individuals and territorial adults, who must allocate additional resources to defend their territories (Amsler, 2010; López-Sepulcre & Kokko, 2005; Low, 2006). Since none of the individuals investigated here started to breed during the study period, further investigation is needed to determine if the trend of increased mobility with age also affects settlement.

The higher mobility observed in winter than in summer can be explained by an increased encounter rate with adult golden eagles as a consequence of food resource overlap. Carcasses are the primary food source for Alpine golden eagles during the first few years after leaving the natal territory as well as for adults during winter (Haller, 1996). Due to the ephemeral yet abundant nature of carcass availability in winter (Jonas et al., 2008), there is likely high spatiotemporal overlap between dominant adults and subordinate transient golden eagles at feeding sites (Jenny et al., 2024; Jenny, 1992), which increases conflict potential. The start of the breeding season in late February could further increase aggression levels of territory holders against intruders, as aggression levels are often elevated around breeding- and chick rearing-time (Landys et al., 2010). The increased spatial overlap between adults and juveniles in combination with higher aggressive levels of adults could thus result in the observed pattern of young birds being more mobile in winter (Palmer et al., 2022), despite the lower availability of environmental uplift in winter compared to summer (Bohrer et al., 2012).

Whether the observed increase in mobility throughout the transience period is primarily driven by an enhanced flight ability, an increase in antagonistic interactions, or a combination of both, remains to be determined. Our findings tentatively support the hypothesis that sexual maturity plays a more significant role in our study system, as the duration of exploration units increased, and encampment got shorter. With both the frequency of intrusion into territories as well as aggression towards intruders escalating with age (Piper et al., 2022), juvenile golden eagles may be increasingly evicted from territories and habitats, resulting in a pinball-like movement pattern across the landscape (Haller, 1996). In contrast, if decreased movement costs were the primary driver, we would expect juveniles to use their acquired knowledge to navigate rapidly, safely, and efficiently around obstacles and social barriers (Stamps, 1995), while optimising time spent in suitable habitat patches (Delgado et al., 2009), thus prolonging encampment periods. Furthermore, research on age-specific mortality causes in golden eagles revealed that 70% of recovered cadavers were three to four years old, with many suffering lethal wounds inflicted by conspecifics (Jenny et al., 2024). Although we were unable to collect comprehensive survival data in this study, the data at hand supports that the probability of fatal interactions with conspecifics increases significantly at around the age of four.

Early-life effect

As expected, the movement patterns of transient individuals were affected by the timing of independence from their parents. Unexpectedly though, early emigrating individuals did not show more pronounced encampment, but prolonged and extensive exploration compared to their late-emigrating conspecifics, and this difference increased with age. The early timing of emigration, indicative of increased cost-effective flight and food conditions experienced in early life (Chapter II; Rotics et al., 2021; Zimmermann, 2021) may induce lifelong cognitive advantages that facilitate movement. Conspecifics growing up under less favourable conditions may never attain the same (Metcalfe & Monaghan, 2001). Malnutrition has been associated with permanent structural changes in the brain, impaired neurocognitive performance (De Rooij et al., 2010; Leroy et al., 2020), altered behavioural responses to adverse conditions (Levitsky & Barnes, 1970), and diminished locomotor capacity (Calado et al., 2024) even at advanced age. It is likely that such early-life deficits may result in permanently reduced cognitive capabilities underlying movement which are necessary for decision making processes (Sergio et al., 2014) to effectively make use of environmental energy (Harel et al., 2016), thus limiting an individual's ability to traverse the highly competitive environment.

Despite having the same biological age, benefits in early life can also make an individual more competitive compared to its peers. We therefore suggest that the early emigrating individuals with the highest mobility and the strongest exploration tendency may also be highly competitive. Traits often related to dominance status and competitiveness include physical characteristics like body size (Moreno-Opo et al., 2020), colouration patterns (Santos et al., 2011), vocalisations (Reby et al., 2005) and behaviours like aggression (Bush et al., 2016) or exploration tendency (Cole & Quinn, 2012; Verbeek et al., 1999). Juveniles exhibiting such traits are often perceived as stronger competitors by territorial adults and this recognition leads to an increased aggression from adults (Landmann & Kollinsky, 1995). Additionally, favourable early-life conditions can lead to earlier sexual maturation (Morgan & Metcalfe, 2001), possibly mediated by a more rapid behavioural development. Competitive juveniles become more focused on securing territories and reproducing at a younger age (Alberts & Altmann, 1995), which could drive them to explore extensively, consequently placing themselves more frequently in conflict situations. Indeed, golden eagles already start showing territorial behaviour at two years old if intraspecific competition is low (Whitfield et al., 2022). In high population densities, mobility could thus indicate that not only first territory establishment is delayed, but also that variation in competitiveness alters the age at which the drive to establish a territory starts to be expressed. Early-life advantages not only have the capacity to boost the inherent competitiveness of juveniles (Royle et al., 2005) but also to prompt a more rapid shift in life-history transitions, thus intensifying interactions with adults and influencing their spatial dynamics within the population (Fero et al., 2007).

We suggest that favourable early-life conditions increase competitiveness and accelerate maturation-related changes in juveniles (Van Leeuwen et al., 2016) is corroborated by the findings that early emigrating individuals first remained more stationary but then changed to become more mobile than their peers. In the first year of transience, early emigrating individuals remained, on average, nearly a full day longer in habitat patches compared to the later emigrating conspecifics. Additionally, the duration of individual encampment units was extended by a day compared to late-emigrating conspecifics. This suggests that more competitive early emigrating eagles have better access to resources or higher quality habitats compared to their peers.

The consequent change in mobility and exploration tendency later in transience was mainly driven by early-emigrating individuals, whose time spent in individual units of exploration increased dramatically between periods of encampment. This indicates that early emigrating individuals are disproportionately and increasingly exposed to interactions with territory holders. Whether those individuals are prevented from remaining encamped or whether they had an inherent drive to actively intrude into territories is still a topic for further investigation. Nevertheless, maturation differences between conspecifics of the same age can significantly alter physical condition, as also shown in humans (Jones et al., 2000). Accounting for potential changes in internal motivation throughout the developmental stages in future studies could deepen our understanding of variability in movement and space use.

Growing up under good conditions does not inevitably result in better performance later in life. Favourable conditions have previously been shown to result in lower survival in red kites, as a mismatch between conditions in early- and late-life means that the behaviours developed were poorly adapted for the later environment (Catitti et al., 2024). Being bolder and more aggressive, and therefore exposed to higher levels of aggression, could ultimately decrease fitness, on top of the presumably higher energetic costs associated with constant movement. Consequently, adopting a more conservative strategy and limiting exposure to conflict might enhance survival and potentially facilitate successful entry into the breeding population. Future research should investigate whether early-life conditions not only alter movement behaviour and space use patterns but also influence survival and reproductive rates, thus yielding insights into the mechanisms through which early life can impact individual fitness and the dynamics of this highly competitive population.

Conclusion

We provide evidence that the timing of early life-history transitions results in permanent changes to the movement behaviour and space use of individuals during transience. Synthesising previous studies with literature linking early emigration to higher fitness in raptors and noting that age-related changes were only observable in individuals emigrating early, we conclude that beneficial early-life conditions can have cascading positive effects on competitiveness and maturation later in life. Although we could not conclusively demonstrate that these changes were directly associated with higher fitness, our findings suggest that early-life conditions may influence which individuals successfully recruit into the breeding population (Richner, 1992) and affect their future reproductive output (Mobley et al., 2020). As parents are highly influential in determining early-life conditions, we assert that the parental quality in a given environment has a massive potential to influence their offspring's competitive abilities and ultimately their recruitment into the breeding population.

4.6 Supporting information

Acknowledgments

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Competing interests

We declare we have no competing interests.

Declaration of originality

We declare we came up with the research question and written the full text ourselves.

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Ethics statement

Catching, ringing and tagging were conducted under the licences of the responsible institutions in the different countries and disturbance was kept to a minimum (CH: Food Safety and Veterinary Office Grisons, permit no. GR 2017_06, GR 2018_05E, GR 2019_03E, GR/08/2021, and the Federal Office for the Environment, licence no. TV201903E; DE: birds were handled, tagged and ringed under the permission issued by the government of Oberbayern (2532.Vet_02-16-88 and 2532.Vet_02-20-86); IT: the permissions for handling, tagging and marking were obtained from autonomous region of South Tyrol (Dekret 12257/2018 and Dekret 8788/2020), as well as from the Regione Lombardia and Sondrio Province for ringing and tagging in Lombardia and South Tyrol by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale) with the Richiesta di autorizzazione alla cattura di fauna selvatica per scopi scientifici (l.r. 26/93).

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4.8 Supplementary material

Table S1. Model estimates for First Passage Time FPT models using alternative radii (2.7, 5.0 and 6.7 km^2). The radii were selected at local maxima of the variance of the log of FPT. Parameter estimates of the Bayesian linear mixed-effects models investigating the effects of emigration timing, age, sex, season and the interactions between age and emigration timing on the movement process (First Passage Time; FPT) and the duration of exploration movement units. Means (Estimates), 95% CrI and Bayesian posterior probabilities (PP; i.e. the likelihood for the given effect size to differ from zero) are given. Effects with a posterior probability ≥ 0.95 are printed in bold and are interpreted as having a strong effect. Model estimates are on the log scale.

		Movement process (FPT)		
Radius 2.7 km^2				
	Fixed Effects	**Estimates**	**95% CrI**	**PP (< or > 0)**
	Intercept	**0.516**	**0.367 to 0.675**	**1.000**
	Emigration timing	-0.009	-0.085 to 0.068	0.586
	Age	**-0.028**	**-0.054 to -0.003**	**0.986**
	Sex (male)	**-0.130**	**-0.266 to 0.003**	**0.972**
	Season (winter)	**-0.131**	**-0.175 to -0.087**	**1.000**
	Emigration timing x age	**0.027**	**0.004 to 0.051**	**0.991**
	Territory ID	0.143	0.016 to 0.250	
	Territory ID : bird ID	0.154	0.065 to 0.248	
	Year of tagging	0.085	0.003 to 0.281	
	Date	0.123	0.111 to 0.136	
Radius 5.0 km^2				
	Intercept	**0.986**	**0.805 to 1.180**	**1.000**
	Emigration timing	-0.011	-0.108 to 0.088	0.582
	Age	**-0.047**	**-0.078 to -0.016**	**0.998**
	Sex (male)	-0.116	-0.298 to 0.059	0.899
	Season (winter)	**-0.165**	**-0.216 to -0.112**	**1.000**
	Emigration timing x age	**0.053**	**0.025 to 0.082**	**1.000**
	Territory ID	0.178	0.015 to 0.310	
	Territory ID : bird ID	0.209	0.106 to 0.323	
	Year of tagging	0.090	0.003 to 0.310	
	Date	0.101	0.090 to 0.112	
Radius 6.7 km^2				
	Intercept	**1.164**	**0.975 to 1.372**	**1.000**
	Emigration timing	0.001	-0.107 to 0.109	0.510
	Age	**-0.057**	**-0.090 to -0.024**	**1.000**
	Sex (male)	-0.064	-0.260 to 0.127	0.739
	Season (winter)	**-0.159**	**-0.213 to -0.104**	**1.000**
	Emigration timing x age	**0.055**	**0.025 to 0.084**	**1.000**
	Territory ID	0.222	0.026 to 0.373	
	Territory ID : bird ID	0.211	0.094 to 0.348	
	Year of tagging	0.089	0.003 to 0.304	
	Date	0.092	0.081 to 0.103	

Table S2. Parameter estimates of the linear mixed-effects model fitted in a Bayesian framework investigating the effects of emigration timing, age, sex, season and the interactions between age and emigration timing on the duration of encampment movement units. Means (Estimates), 95% CrI and Bayesian posterior probabilities (PP; i.e. the likelihood for the given effect size to differ from zero) are given. Effects with a posterior probability ≥ 0.95 are printed in bold and are interpreted as having a strong effect. Effects with a posterior probability > 0.90 and < 0.95 are printed in itlaics and are interpreted as having a weak effect. Model estimates are inversely transformed.

	Encampment duration		
Fixed Effects	**Estimates**	**95% CrI**	**PP (< or > 0)**
Intercept	**0.187**	**0.167 to 0.205**	**1.000**
Emigration timing	0.001	-0.007 to 0.010	0.628
Age	**0.006**	**0.000 to 0.013**	**0.980**
Sex (male)	0.006	-0.010 to 0.023	0.778
Season (winter)	0.001	-0.010 to 0.011	0.545
Emigration timing × age	*-0.005*	*-0.011 to 0.001*	*0.945*
Random Effects			
Territory ID	0.009	0.000 to 0.022	
Territory ID : Individual ID	0.015	0.003 to 0.026	
Year of tagging	0.011	0.000 to 0.035	

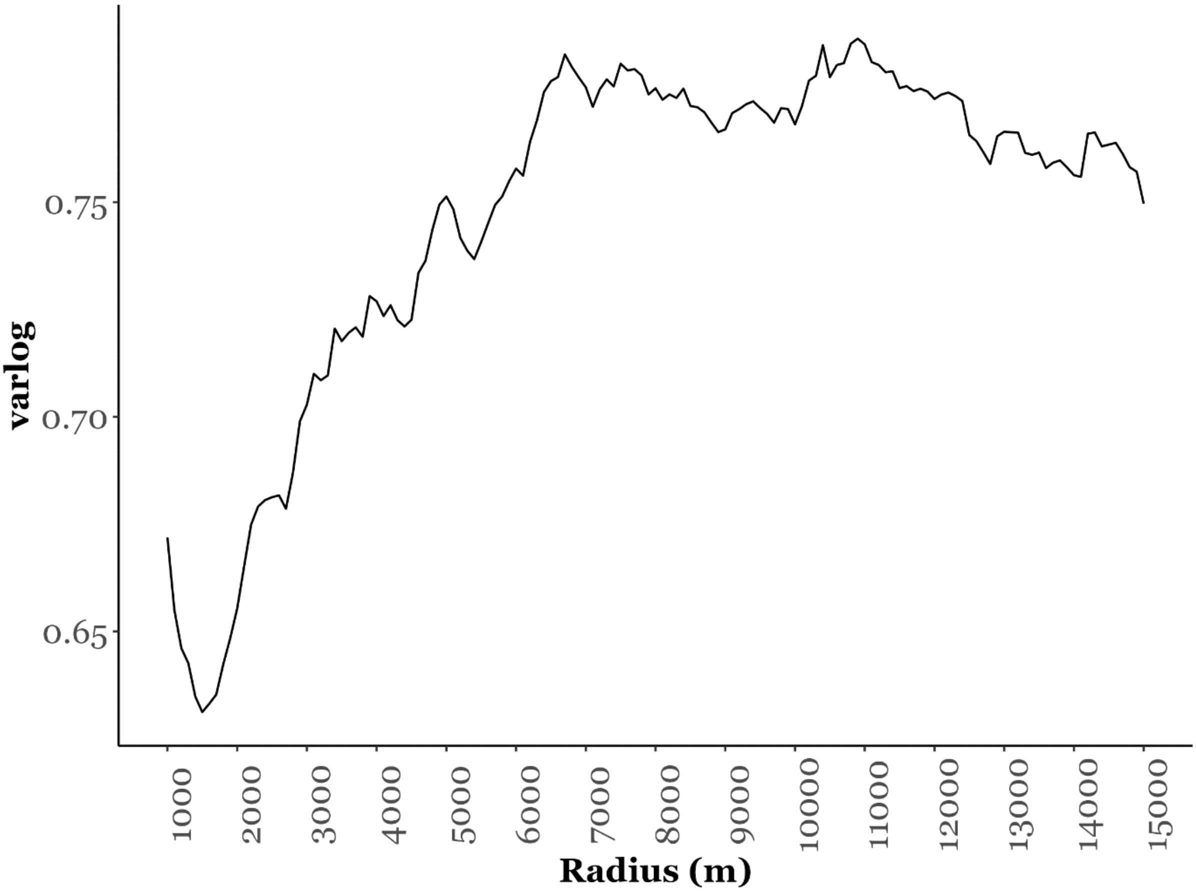

Figure S1. Variance of the log of First Passage Time FPT for different radii. Local maxima of the variance indicate scales at which patterns occur in the trajectory (e.g. area restricted search).

5. Chapter IV

Territoriality in a dense population affects where pre-breeders can roost

Julia S. Hatzl[a,b], Steffen Oppel[a], Enrico Bassi[c,d], Jérôme Guélat[a], David Jenny[a], Florian Orgeret[a], Loïc Pellissier[b,e], Kamran Safi[f], Matthias Tschumi[a], Martin U. Grüebler[a]

Illustration: Lara Gross

Affiliations

[a] Swiss Ornithological Institute, Sempach, Switzerland.
[b] Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland.
[c] Vulture Conservation Foundation Advisory Board, Zurich, Switzerland.
[d] Italian Ornithological Studies Center CISO.
[e] Unit of Land Change Science, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland.
[f] Max Planck Institute of Animal Behavior, Radolfzell, Germany.

E-mail addresses and ORCIDs of co-authors:

J. S. Hatzl: julia.hatzl@vogelwarte.ch; ORCID**: 0000-0002-7915-9588**
S. Oppel: steffen.oppel@vogelwarte.ch; ORCID: 0000-0002-8220-3789
E. Bassi: enrico.bassi76@gmail.com; ORCID: 0000-0002-0698-4800
J. Guélat: jerome.guelat@vogelwarte.ch; ORCID: 0000-0003-1438-4378
D. Jenny: jenny.d@compunet.ch; ORCID: 0000-0003-3027-0004
F. Orgeret: florian.orgeret@vogelwarte.ch; ORCID: 0000-0002-1940-7797
L. Pellissier: loic.pellissie@ethz.ch; ORCID: 0000-0002-2289-8259
K. Safi: ksafi@ab.mpg.de; ORCID: 0000-0002-8418-6759
M. Tschumi: matthias.tschumi@vogelwarte.ch; ORCID: 0000-0002-7991-7780
M. U. Grüebler: martin.gruebler@vogelwarte.ch; ORCID: 0000-0003-4468-82

Keywords

Habitat selection, social environment, pre-breeder, saturated population, transience, movement behaviour

Chapter notes

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Authors contributions

J.S.H., M.U.G. and S.O. conceived the idea. J.S.H., K.S., D.J., E.B. carried out the fieldwork. J.H. conducted the formal analysis. Methodology was developed by J.S.H., M.U. G., L.P., S.O., M.T., K.S., D.J., F.O.; J.S.H. wrote the first draft of the manuscript and all authors contributed substantially to the revisions.

5.1 Abstract

Territoriality is a consequence of competition over resources and creates a specific social environment to which all individuals of a species are exposed to. Since pre-breeding juveniles are often excluded from existing territories, saturated populations with adjacent territories leave only limited space for the pre-breeding part of the population. It remains an open question as to how pre-breeding juveniles navigate the social environment of territoriality to survive until recruitment. Here, we combine GPS-tracking data of a large raptor species (golden eagles, *Aquila chrysaetos*) with an extensive, independent dataset of eagle territories within Switzerland to understand the effects of the social environment on the space use of pre-breeding individuals. We investigated the effects of distance to territory centres and territory borders on overnight roost site selection of pre-breeders while accounting for landcover and topographic variables. We further examined whether the role of territorial variables differed in habitat selection between day and night, and between exploratory (exploration) and area-restricted (encampment) movement behaviours. We found that pre-breeding golden eagles avoided central areas of territories and selected areas close to territory borders, both during night and day. Roosts during periods of encampment were much farther from territory centres than roosts that were used during periods of exploration. Our study provides insights into the poorly understood pre-breeding life stage and highlights that the social environment of territoriality affects the spatial distribution of young individuals during natal dispersal and therefore represents an important factor driving density-dependent recruitment processes.

5.2 Introduction

Movement enables animals to access scattered resources in the physical environment, but by exhibiting territorial behaviour, individuals regularly exclude conspecifics from accessing resources (Brown & Orians, 1970). This creates a specific social environment to which all individuals of a species are exposed to. Territoriality is the consequence of competition over limited resources (Börger et al., 2008; Burt, 1943; Maher & Lott, 1995) and is often associated with the Ideal Despotic Distribution Hypothesis (Brown, 1969; Oro, 2008), which states that dominant individuals restrict conspecifics from accessing high quality habitats. Thus, by forming a landscape with potential for high social conflict and dominance, territoriality represents a key mechanism underlying animal movement in many species (Maher & Lott, 2000). Studying the effects of territoriality on space use can therefore improve our understanding of ecological and demographic processes (Morales et al., 2010; Nathan et al., 2008).

Territoriality is a costly behaviour and only evolves when the benefit of defending resources like food, mates or breeding sites outweigh the associated costs including aggression, risk of injury and energy expenditure (Brown, 1964). Typically, when controlled for the environment, territory size decreases with increasing population density (Sells & Mitchell, 2020; Stenger, 1958). As the number of territories increases, so does the probability of agonistic interactions associated with territoriality (Webber et al., 2023), with consequences at the individual (e.g. stress physiology (Creel et al., 2013), population and community level (Carrete et al., 2006; Weiner et al., 2019). Territory number continues to increase until a saturation point is reached where the available resources cannot support an even higher number of territories (Hartmann et al., 2017; Turchin, 2001). In this situation, dispersing individuals can either emigrate to other populations (Cote et al., 2017; Matthysen, 2005) or try to recruit into the saturated population. For young individuals in particular, the strategy to remain in the saturated population requires them to navigate within a highly aggressive social environment to acquire the necessary resources for survival (Hinsch & Komdeur, 2017). The social environment is therefore an important driver of dispersal movement (Matthysen, 2005), space-use of individuals (Eisaguirre et al., 2022; Hansen et al., 2024) and emigration patterns (Clobert et al., 2012; Pasinelli & Walters, 2002; Wey et al., 2015), with crucial consequences for population level processes (Matthysen, 2005).

In species showing cooperative breeding, young individuals may stay for prolonged periods as helpers within parental territories (Cornwallis, 2018; Rubenstein & Abbot, 2017). Juveniles of non-cooperative breeders must leave the parental territory by the end of the parental dependency period, entering the transience period of natal dispersal (Bowler & Benton, 2005; Clobert et al., 2012) In long-lived species, this transience or wandering period can last for multiple years. Dense populations often show a prolonged transience period and thus, delayed recruitment. Recruitment might occur long time after sexual maturity is reached (Whitfield et al., 2022; Zack & Stutchbury, 1992). Throughout the transience period pre-breeding dispersers have to meet their daily needs, but they also acquire information about territories (Cozzi et al., 2018; Oro et al., 2021; Reed et al., 1999) and gain experience in social interactions and movement skills (Cortés-Avizanda et al., 2014; Nourani et al., 2024; Chapter III). However, dispersal is also associated with considerable costs (Bonte et al., 2012). Moving through a dense territorial landscape might be costly in terms of increased energetic demands and stress levels due to aggressive encounters (Young & Monfort, 2009). Thus, dispersers are expected to reduce aggressive interactions with territory owners, which leads to a delicate trade-off between finding suitable habitat without being detected by territory holders (Bruinzeel & Van De Pol, 2004). The spatial restrictions and the high costs associated with persisting within a saturated population raise the question as to how future recruits of the breeding population are distributed in the landscape—and what environmental and social characteristics affect their distribution.

Pre-breeding individuals during transience typically exhibit a combination of fast, large-scale exploratory movements (exploration) and slow, spatially restricted movements (encampment), which are often associated with temporary home ranging behaviour (Delgado & Penteriani, 2008; Fryxell et al., 2008; Killeen et al., 2014). These two contrasting movement behaviours (Nathan et al., 2008) are often put into context with exploratory between patch movements and area-restricted within patch movements (Owen-Smith et al., 2010), reflecting changes in the interplay between intrinsic and extrinsic factors (Nathan et al 2009). Performing such different behaviours requires different resources, resulting in behaviour-dependent habitat selection (Ellington et al., 2020; Northrup et al., 2022; Séchaud et al., 2021), also in terms of the social environment (Wittemyer et al., 2007). During exploration, habitat characteristics enabling efficient movement might be preferred, even if this means tolerating a higher risk of predation or agonistic encounters compared to encampment (Dickie et al., 2023). In contrast, home ranging behaviour during encampment can occur in areas with increased resource availability (McLoughlin et al., 2010), but where risks are lower (Beumer et al., 2023; Roever et al., 2014; Séchaud et al., 2021). Therefore, understanding the effect of territoriality on habitat selection of young animals during transience requires considering these two different movement behaviours (Roever et al., 2014).

The strong year-round territorial system in the dense Alpine population of the golden eagle, *Aquila chrysaetos* (Haller, 1996; Jenny et al., 2024), a widely distributed avian apex predator (Ellis et al., 2024), provides an ideal model to study habitat selection in a saturated population. Territories are defended vigorously against intruders (Jenny, 1992) and pairs are strongly bound to the part of the territory in which the nesting sites are located throughout the year (Eisaguirre et al., 2022; McLeod et al., 2002). Juveniles leave the parental territory a few months after fledging (Chapter II; Zimmermann, 2021) and roam the Alps for multiple years (Haller, 1996; Chapter III; Whitfield et al., 2022)—a period to which we refer to hereafter as the 'pre-breeding' period. Before recruiting dispersing pre-breeders alternate between large-scale exploration and encampment throughout transience (Chapter III). Recruitment of golden eagles into the breeding population is strongly delayed due to the high population density prevailing in the entire Alpine range (Haller, 1996; Whitfield et al., 2022). Studies on habitat requirements have mainly targeted adult settlers (Haller, 1996; Maynard et al., 2024), whereas habitat selection of pre-breeders has hardly been considered (Eisaguirre et al., 2022), despite the crucial implications of the social environment for recruitment processes.

Here, we combine an extensive dataset of GPS-tracked juvenile golden eagles with a map of breeding territories based on observations of territorial behaviour to explore the effect of territoriality on pre-breeder habitat selection during transience in a saturated population. We first investigated the effect of the social environment of territories on overnight roost site selection of pre-breeders, while accounting for topographic and habitat variables. We focussed on overnight roosts as they are expected to be most sensitive to agonistic disturbances because individuals are exposed for an extended period of time (Hendrichsen et al., 2006; Peters & Otis, 2007). We expected that pre-breeders select roost sites far from territory centres to reduce agonistic interactions with residents while still selecting high-quality habitats. We then tested whether the effect of the social environment on habitat selection differed between nocturnal roosts and diurnal locations, with the expectation that the avoidance of territory centres was reduced during the day. Lastly, we investigated whether the social characteristics of roost sites differed between periods of exploration and encampment, expecting that roost sites during encampment were in larger distance to territory centres compared to roost sites during exploration due to lower risk of encountering interactions with breeding pairs (Jenny, 1992; McLeod et al., 2002). With our study we contribute to the understanding of spatial processes driven by the social environment of year-round territoriality in saturated populations.

5.3 Methods

Study species

Golden eagles are widely distributed throughout the Holarctic (J. Watson, 2010) and inhabit a variety of different habitats with low anthropogenic disturbance. However, in central Europe, increasing human activity and development of lowland areas have led to habitat loss, forcing the non-migratory population of golden eagles to retreat predominantly to mountainous and alpine regions (Jenny et al., 2024). The intense persecution of golden eagles reduced breeding pair numbers substantially up to the middle of the nineteenth century also within the alpine regions (Haller 1996). Today, the population has recovered and approximated a saturation point (Haller, 1996; Jenny et al., 2024), where no suitable breeding habitat remains unoccupied. The entire Alps are densely covered by abutting territories (figure S1), inhabiting about 1.4 pairs per 100 km^2 in Switzerland and hardly any new territories established in the last decade (Jenny et al., 2024). Territories are maintained and defended year-round, territory borders are virtually stable (Potts et al., 2012), and each territory includes multiple nest sites which can be used alternatingly between years (Haller, 1996; Jenny et al., 2024). Juvenile golden eagles generally emigrate from the parental territory between September of their birth year and April of the following year (Hatzl, 2024; Zimmermann, 2021). After emigration, juveniles then enter an extensive pre-breeding transience period before settling in a territory and recruiting into the breeding population at five years or older (Jenny et al., 2024).

Movement data

We tagged 46 nestlings at an age of c. 50 ± 3 days between 2017 and 2023. We aged nestlings by assessing plumage development. Nests were situated in Switzerland and Italy (for details on the tagging procedure and the data collection regime see Chapter I and II). GPS tags (e-obs solar powered tags, 25 or 45 g) recorded bird locations in a flexible time interval dependent on the battery charging level. GPS recording interval ranged from every second to once a day until a bird died (n = 9), technical failure of the tag (n = 9), tag loss (n= 9) or until the end of our study period in April 2024 (n = 22).

Social environment

To extract variables of the social environment of territories, we used an existing comprehensive layer of 369 breeding territories and nest locations (figure S1) (Jenny et al. 2024; Knaus et al. 2018; Monitoring Swiss Ornithological Institute; Grisons Fish and Game Department) in Switzerland. Nest information was obtained from monitoring data of the Swiss Ornithological Institute as well as from recordings in the observational database ornitho.ch (Monitoring Swiss Ornithological Institute; Grisons Fish and Game Department). Within each territory we drew a Minimum Convex Polygon (MCP) around 80% of all recorded nest sites and derived the nest centroid as the centroid of this polygon (hereafter referred to as 'territory centres'). For one territory we derived the territory centre as the centroid of the territory polygon because we did not have any nest recordings for that territory.

Topography and habitat variables

Including a set of landcover and topographic variables allowed us to assess the basic requirements of roosting sites, such as predator safety and accessibility. We selected the habitat variables based on the findings of previous studies investigating habitat selection of territorial golden eagles (Haller, 1996; Maynard et al., 2024). Landcover information was obtained from the Swiss Landuse Statistics (Federal Statistical Office) with a 100 × 100 m resolution, which we grouped into four classes that were relevant to golden eagles: "Unvegetated", "Open vegetation", "Forests", "Anthropogenic landscape". An additional category "Other" included the landcover type "Waterbodies" which we expected not to be important for golden eagle habitat selection and thus it was not included in the analysis (see table S1 for detailed descriptions of variable groupings). "Unvegetated" represented areas where thermal currents can build up and offer thermal uplift that facilitates energy-efficient travelling for soaring birds. The "Open vegetation" incorporated landcover types of low vegetation height or extensively managed grassland which represent good foraging grounds where the main prey species marmot (*Marmota marmota*), grouse (*Tetraoninae*) and ungulates occur (Haller, 1996; Regos et al., 2021). While "Forests" offer limited feeding opportunities, they provide valuable shelter to avoid detection by territorial eagles. "Anthropogenic landscape" indicates areas of high human disturbance that eagles typically avoid. We calculated the proportion of each landcover type in a 250 m and a 1'500 m radius around each GPS location, as eagles may assess landscape composition at varying scales. Alternative radii of 50 and 500 meters yielded consistent results.

We obtained topographic variables from a digital elevation model (DEM) (DHM25 © swisstopo) at a 25 × 25 m resolution and resampled them to a 100 × 100 m resolution to match the resolution of the landcover data. From the resampled DEM we extracted average elevation (meter above sea level), and generated slope (degrees), northness (radians), eastness (radians) (Roberts, 1986), and the Terrain Ruggedness Index (TRI). TRI represents a measure for landscape roughness and was calculated as the square root of the sum of the squared differences between the elevation in a cell and the elevation of its neighbouring cells (Riley, DeGloria, and Elliot 1999) using the function 'terrain' of the 'terra' package (Hijmans 2023). High TRI values are a valid predictor for locations where uplifts occur (Nourani et al., 2024; Scacco et al., 2019) and were found to be influential for the movement of soaring birds (Sur et al. 2019). All extractions and analyses were done using the statistical software R, version 4.2.1 (R Core Team, 2020).

Concept of analyses

We approached the analysis of the effects of the social environment on habitat selection by analysing overnight roost sites (hereafter 'roost sites') using machine learning algorithms. In a first step, we compared roost site and random available sites, to assess how juveniles select overnight roosts relative to available habitat options and to evaluate the relative influence of social and environmental factors. In a second step, we invested differences between roost sites and daytime locations to determine whether the influence of the social environment, particularly the avoidance of territory centres, differs between night and day. In a third step, we analysed the environmental differences between roost sites during encampment and roost sites during exploration within the general roost site selection to explore how juveniles adjust their roost site selection according to their behavioural state, with a focus on the trade-off between territory avoidance and habitat quality.

We focused our analysis specifically on roosting behaviour because, at a fine scale, animals engage in variety of behaviours such as flying, feeding, roosting. Including this wide range of behaviours could introduce variability, potentially obscuring the patterns we aimed to investigate (Roever et al., 2014). Additionally, territorial behaviour is expected to have a larger effect on roost site selection than on daytime habitat selection of pre-breeders: aggressive interactions during roosting are energy demanding and dangerous, while daytime locations of the highly mobile non-territorial pre-breeders might occur also regularly within territories. Birds can cross territories at very high flight heights with low exposure risk to agonistic interactions with breeding pairs. Thus, the effect of the territorial social environment is likely lower during daytime, when high mobility and varied behaviours lead to different habitat selection dynamics.

Modelling habitat selection

For modelling habitat selection (first step), we only used movement data within Switzerland, because detailed information on territorial boundaries was not available for adjacent countries. We also limited the data for each individual to the time after emigration from the parental territory (for emigration dates, see (Chapters I and II; Zimmermann, 2021) and extracted the last daily location (between 19:00 and 20:00 UTC) from the trajectories as overnight roost sites. We retained all roosts after emigration as no individual settled permanently and initiated breeding up to the end of our study. For each roost site (used) we created 10 random locations that an individual could have used as roost (available) which we randomly generated within an individuals' movement range (80% Minimum Convex Polygon of roost sites of the individual within the borders of Switzerland. Then, for each used and available point, we extracted the explanatory environmental variables from above.

In the second step, we compared each overnight roost site (used) to up to 10 random daytime locations (available) of the same individual that preceded the overnight stay between 10:00 and 15:00 UTC.

In the third step, we investigated how environmental and social variables differed between roosts according to the underlying behavioural state—encampment and exploration. We classified overnight roost sites as either encampment (with at least 3 nocturnal roosting incidents within a 3.9 km radius) or exploration (a maximum of 2 roosting incidents of the same individual within a 3.9 km radius) using a previously developed behavioural segmentation algorithm (Chapter III). We segmented the movement trajectory into the two discrete movement behaviours—encampment and exploration—by first calculating First Passage Time FPT, a measure for area use intensity (Fauchald & Tveraa, 2003). Breakpoints in the FPT time series, indicative of a change in movement behaviour, were identified using Lavielle's segmentation method (Lavielle, 1998). The algorithm could not assign 14 locations to a behavioural phase as they were solitary locations collected during times of poor data collection which we therefore removed from this analysis. After classification, he encampment-to-exploration ratio was approximately 1:2.

For all three steps we used a random forest modelling approach. Applying a random forest (Evans and Cushman 2009) to quantify habitat selection allowed us to simultaneously account for a large number of explanatory variables and their interactions (Breiman, 2001; Cutler et al., 2007). We fitted each model using the R package 'randomForest', version 4.7-1.1 (Liaw & Wiener, 2002) and used the default parameters except the number of trees grown and number of variables used at each split. For each random forest we determined the optimal values for the number of trees (ntree = 1'500) and variables used at each split (mtry = 3) from varying configurations until accuracy maxed out using the package caret, version 6.0-94 (Kuhn, 2008). When growing each forest of each model, we maintained a 1:1 ratio between the roost sites of both classes (used vs. available; night vs. day; encampment vs. exploration) by randomly subsampling sites from the overrepresented class to avoid problems with class-imbalance (He & Garcia, 2009). Each model was repeated 50 times, each with a different random subsample.

We included the same predictor variables for all three models. In addition to the topographic and habitat type variables (elevation, slope, TRI, northness, eastness, and proportions of unvegetated area, open vegetation, forest, anthropogenic landscape, other habitats), we extracted two variables explaining the potential effect of the social environment from the territory layer for each used and available site: the distance to the next territory centroid and the distance to the next territory border. We multiplied the distance to the territory border at sites outside of territories by –1 to create a continuous metric where agonistic interactions would be more likely with an increasing value of this distance. The lack of information about territories outside of Switzerland could, however, bias the distance values between our eagle roost sites (in Switzerland) and nest centres. Roosts close to the Swiss border can be much closer to a territory centre outside of Switzerland than to the nearest territory centre within Switzerland. To reduce the potential effect of this bias we excluded datapoints which were close to the Swiss border (half of the mean distance between territory boundaries and nest centres) and were far away from territory centres (95% quantile of the distance to the nearest territory centre). We therefore excluded 13% of the roost sites, 11% of the random available sites, and 13% of the daytime locations from our dataset.

Model validation and interpretation

To evaluate model performance, we first assessed predictive performance with 20% of the of the data of the individuals used to train the forest in a cross-validation but that was not used to train the models. To ensure that the model is not overfitting we also evaluated model performance with data from six individuals not used for model training. We randomly selected six individuals from the pool of individuals contributing the least (three individuals) and the most (three individuals) data to the whole dataset (10% quantile = 5 individuals; 90% quantile = 4 individuals). Such blocked-individual validation allowed us to obtain conservative error estimates by having independent test data from different individuals (Araújo et al., 2005; Roberts et al., 2017; Soley-Guardia et al., 2024).

When evaluating and reporting the predictive power of each model, we applied the same class-balancing procedure to the independent validation data as was used for training the model. For each model, we reported the average values of overall accuracy (0 = no datapoints correctly identified, 1 = all datapoints correctly identified), sensitivity (0 = no true positives identified, 1 = all true positives identified), specificity 0 = no true negatives identified, 1 = all true negatives identified) and kappa (-1 = classification/prediction complete disagreement, 1 = classification/prediction complete agreement) calculated over all 50 random forests (R package ‘rfUtilities’, version 2.1-5). Standard deviation for all metrics was < 0.1. For each question, we reported model evaluation metrices for the two independent validation datasets (independent cross-validation, blocked-individual). In addition to the above-mentioned evaluation metrics, we calculated the True Skills Statistics (TSS) (0 = performance no better than random, 1 = perfect classification) to evaluate model performances as it is an intuitive measure of model performance (Allouche et al., 2006). For the roost site selection model (step 1), we additionally calculated the Boyce index to evaluate predictive power of presence only data because all of the randomly generated ‘available’ points could have in theory also been used as roosts by other, untagged individuals (Boyce et al 2001, Hirzel et al 2006).

To assess which variables had the greatest influence on habitat selection we reported the mean decrease in accuracy when permuting each variable using the 'importance' function (R package 'randomForest'). Relative variable importance was derived from the reduction in discriminative ability and was scaled to 100% for the most important variable. We reported the variable importances of one of the 50 random forests grown per question as they were highly comparable (detailed output in table S1). We derived partial plots to visualise the relationship of each predictor with the response variable. We presented these relationships for tow social environment variables for the model comparing roost sites vs available sites and roost sites during encampment vs roost sites during exploration. For each predictor variable we drew 200 samples between the minimum and maximum values and predicted the response value using the package 'pdp', version 0.8.1 (Greenwell, 2017).

5.4 Results

To analyse roost site selection of pre-breeding golden eagles, overnight roost sites (n = 12’573) from 46 individuals were available. Individuals were tracked for up to 4.5 years between 2018 and 2024. On average, individuals were tracked for 1’327 ± 892 days (mean number of days within Switzerland = 273 ± 331; range: 3 – 1’259). Overall, the tracked pre-breeding golden eagles visited a total of 222 of the 369 occupied golden eagle territories in Switzerland, with each tracked individual visiting on average 38 ± 28 territories during the pre-breeding period (range = 2 – 114 territories). Across all individuals, 50% of all roost sites were located outside of Switzerland (mean per individual = 321 ± 296, range= 4 – 1’279). Pre-breeding dispersers roosted on average at a distance of 1023 ± 849 m (range = -1’280 – 4’465 m) from the nearest territory border and 3471 ± 1502 m (range = 69 – 6’901 m) from territory centres. For comparison, the mean size of breeding territories was 65 km^2 ± 28 km^2 (range = 17 – 215 km^2) and the distance between nest centre and the nearest territory border ranged from 183 to 7’160 m (mean = 2’193 ± 989 m). On average, tracked pre-breeding individuals roosted at elevations of 1995 ± 480 m (range = 610 – 3’421 m) and on hillsides with an average slope of 35 ± 9% (range = 0 – 66%).

Pre-breeding dispersers roosted fewer times in encampment (3’705 overnight roosts) compared to exploration (8’853 overnight roosts). Individuals spent on average 27 ± 20% of the recorded roosts in encampment (range = 0 – 82% of roosts in encampment). Roost sites during encampment were in similar distance to territory centres (mean = 3731 m; SD = 1’469 m; range = 103 – 6’899 m), compared to roost sites during exploration (mean = 3’362 ± 1503 m; range = 69 – 6’901 m), and the distance to territory borders was almost identical (encampment: mean distance = 1’016 ± 841 m; range = -1’053 – 4’370 m; exploration: mean distance = 1’027 ± 853 m; range = -1’280 – 4’465 m).

Overnight roost site selection

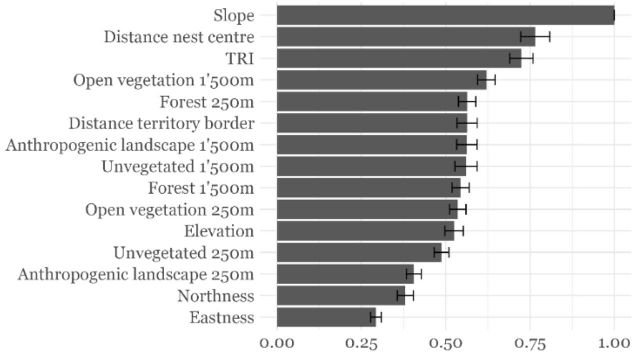
For the first step, our random forest model accurately distinguished between used roost sites and random available sites (table 1, Boyce Index = 1), and correctly predicted 74% of roost sites of the independent cross-validation data and 73% of roost sites in independent test individuals.

Table 1. Performance statistics for random forest models explaining the overnight roost site selection of golden eagles in Switzerland. The first modelling step compared overnight roost sites (1) against randomly sampled available sites (0) within everyone's movement range. The second modelling step compared overnight roost sites (1) against daytime locations (0). The third model explored the differences between roost sites during two distinctive behavioural modes, encampment (1) exploration (0). We reported the mean per model evaluation of all 50 random forests ran.

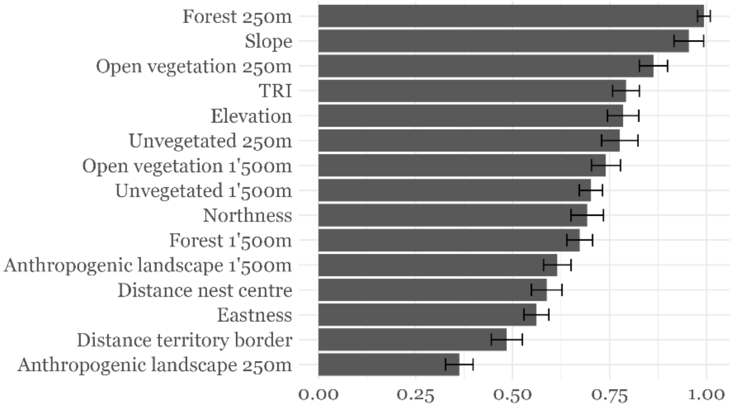
		Overall accuracy	Kappa	Sensitivity	Specificity	TSS
Overnight roost site vs random available locations	Cross-validation testing data	0.74	0.49	0.71	0.78	0.49
	Blocked-individual validation data	0.73	0.47	0.70	0.76	0.47
Overnight roost site vs daytime locations	Cross-validation testing data	0.61	0.23	0.61	0.62	0.23
	Blocked-individual validation data	0.59	0.19	0.54	0.64	0.19
Encampement vs exploration	Cross-validation testing data	0.65	0.30	0.69	0.61	0.30
	Blocked-individual validation data	0.59	0.14	0.67	0.48	0.14

Steepness of slopes and distance to the nearest nest centre were the most important variables explaining where pre-breeding golden eagles roosted (figure 1A), whereas landcover types were less important. Roost sites occurred mainly in areas with slopes steeper than 40%, close to the nearest territory border but at slightly large distance to territory centres (figure 2A-B; figure S2). Anthropogenic landscape features were avoided at large spatial scales (1'500 m), and therefore were not important at smaller scales (250 m, figure S2). Exposition (northness and eastness) appeared to be unimportant for roost site selection.

(A) Overnight roost site vs random available location



(B) Overnight roost site vs daytime location



(C) Roost sites during encampment vs roost sites during exploration

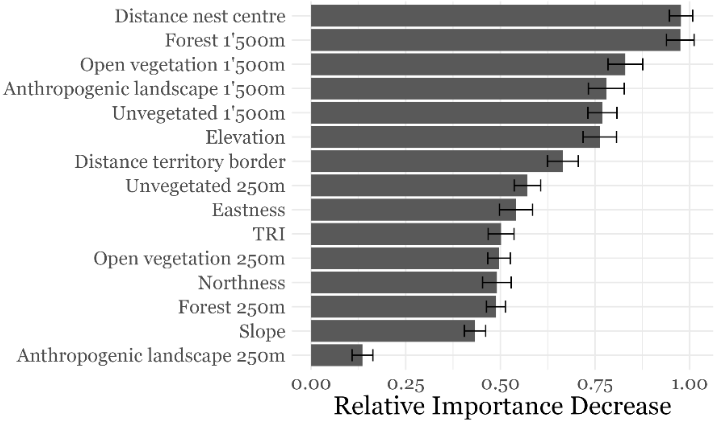


Figure 1. Relative variable importance of the predictor variables in the three modelling steps analysing habitat selection of pre-breeding golden eagles in Switzerland. Random forest model investigation (A) roost sites vs random available sites, (B) roost site vs daytime sites, and (C) roost sites during encampment vs roost sites during exploration. Variable importance was derived from a permutation procedure quantifying the reduction in discriminative ability of a random forest model, and is scaled to 100% for the most important variable. Represented is the mean (solid box) and standard deviation (error bar) of the variable importance calculated using 50 Random Forest models per question, each trained with a different balanced subset of data.

In the second step, the model comparing nocturnal and diurnal locations showed a lower ability to differentiate between roost sites and daytime locations (accuracy independent cross-validation = 0.61; accuracy independent test individuals = 0.59; table 1). This indicates that roost sites were more similar to daytime locations than to random locations. While variables associated with the social environment (distance to territory centre, distance to the nearest territory border) contributed little to explain any differences between roost sites and daytime locations, the most important variables were habitat and topographic variables (forest, 250 m; slope; elevation, figure 1B). In particular, daytime locations occurred in areas with a lower coverage of forest, and in generally less steep terrain than roost sites (table S1).

Comparison of roost sites during mobile and encamped movement periods

In the third step, the models investigating the environmental differences between roost sites during encampment and roost sites during exploration also had limited explanatory power, classifying 65% of roosts correctly in the independent cross-validation data but only 59% of roost sites in independent test individuals (table 1).

Roost sites during encampment and exploration differed in their location within the social environment, the surrounding landcover as well as in elevation. Roost sites farther away from territory centres were more likely to be used during encampment (figure 2C). Roost sites that were far outside existing territories were more likely to be used during exploration, whereas roost sites were most likely to be used repeatedly during encampment at locations that balanced the trade-off of good habitat within territories but low exposure to aggression far away from territory centres (figure 2D).

Roost sites at lower elevations (below 2’000 m) were more likely to be used during encampment. Overall, landcover composition on a large spatial scale appeared to have a stronger explanatory power discriminating roost sites than landcover composition at small spatial scales. Roost sites with a forest cover less than 50% and predominantly covered by open vegetation in a 1’500 m radius were more likely to be used during encampment (figure 1C, figure S2).

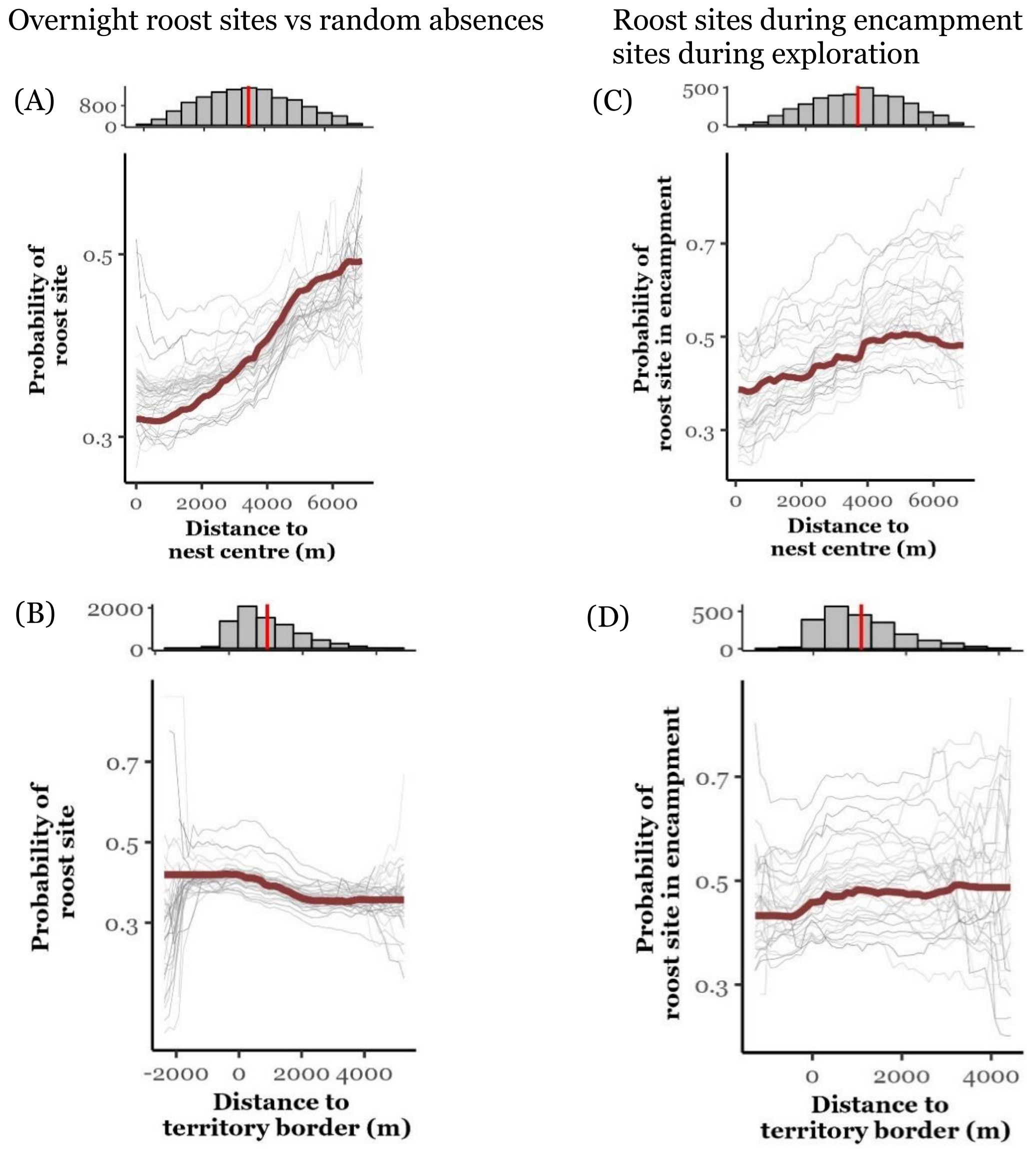


Figure 2. Predicted partial effects of social environmental variables (distance to nearest nest centre and territory border) on the probability of pre-breeding golden eagles in Switzerland roosting overnight at a given site. Negative values of distance to territory border indicates areas outside the territory whereas positive values indicate areas inside the territory. Left (A-B): Probability of a roost site (1) compared with randomly sampled available locations (0). Right (C-D): Probability of a roost site during encampment (≥ 3 nights; 1) compared with a roost site during exploration (< 3 nights; 0). We predicted the partial effect of each predictor over the range of observed values (n = 200 per variable) while holding all other predictors at their means. Red line indicates the population mean and light grey lines indicate predictions for each individual bird. The histogram above each predictor plot represents the distribution of used (1) roosting sites with the vertical red line indicating the mean.

5.5 Discussion

We show that the social environment of territoriality has crucial effects on habitat selection and the distribution of pre-breeding individuals during transience. Pre-breeder golden eagles consistently avoided areas near territory centres and selected areas around the borders of territories, both at night when roosting and during daytime activities. Within this general selection pattern, roost sites during encampment were mostly far away from territory centres in open areas within territories, whereas roost sites during exploration occurred closer to territory centres, but in more forested areas just at the territory borders. These results suggest that the avoidance of agonistic territorial interactions shapes roosting and range use behaviour of non-territorial, pre-breeding individuals in the population, and that roost site characteristics vary according to the movement behaviour. Territoriality thus reduces space and resources available to pre-breeding individuals, with only a few sites suitable to stay for longer periods during encampment.

Pre-breeding golden eagles generally avoided areas near territory centres, preferring border regions of territories instead. This pattern likely resulted from the spatial distribution of agonistic behaviour of territory holders (Carazo et al., 2008; Giraldeau & Ydenberg, 1987). Adult territorial golden eagles concentrate their activities in core areas of their territories, typically near nesting sites that offer good uplift conditions, food availability, and low disturbance levels (Eisaguirre et al., 2021; Maynard et al., 2024; Watson et al., 2014). The frequent presence of adults (Giuggioli et al., 2011) coupled with an elevated intensity of agonistic behaviour in core areas (Carazo et al., 2008; Giraldeau & Ydenberg, 1987; Schradin, 2004) likely leads to significant costs and risks for pre-breeders when entering core areas. Costs include increased energy expenditure for escape or fight (Riechert, 1988; Williams et al., 2020), but also increased stress levels (Creel et al., 2013; Gallagher et al., 2017) and high risks of injuries (Jenny et al., 2024). Our results suggest that these costs may be higher than the benefits of intruding core areas of territories. The avoidance behaviour results in a spatial segregation between adult territory holders and leaves pre-breeders to occupy the interstices between territories (Eisaguirre et al., 2022; Haller, 1982). Thus, the available space for pre-breeders in our saturated population is restricted to the few gaps between territories, to narrow areas at the border between territories, and to less defended parts of territories outside core areas. Our study highlights that meeting the fundamental requirements in a saturated population might be challenging for young birds because much of the available habitat is dominated by territory holders.

The low importance of variables of the social environment for discriminating between day and night locations indicates that pre-breeders were affected similarly by territory holders both at selecting overnight roosts and during daytime activities. However, the high importance of topographic and habitat variables shows that within the limited space available to pre-breeders, the overnight roost sites must be selected carefully. Roost sites were situated in more forested patches at the northern sides of valleys. Pre-breeders roosted at elevations of about 2’000 m with slopes of around 40% and medium TRI values. In contrast, daytime locations occurred across the whole range of slopes, TRI values and elevations. The proportion of open vegetation cover higher at southern sides of valleys where pre-breeders also occurred during daytime but such habitats were rarely used at nighttime. Open and half-open areas represent the typical habitat of the golden eagle's main prey, such as Alpine marmots (*Marmota marmota*), several grouse species (*Tetraoninae*), and large ungulates and thus are preferably used for foraging (Haller 1996). Even though high TRI values, sunny southern exposed slopes and mountain rims have been associated with good uplift conditions and thus are essential for energy-efficient movement for soaring birds (Murgatroyd et al., 2018; Nourani et al., 2024; Scacco et al., 2023), pre-breeding eagles often show large-scale movements and engage in a variety of behaviours throughout the day (Chapter II; preliminary analysis). During these movements they cross valleys with flat, low-elevation valley bottoms, as well as highest mountain tops to forage, engage in locomotor play or socially interact. Thus, high variation of behavioural activities and large-scale movements of eagles during daytime results in using a much larger topographic and habitat spectrum than use for roosting where habitats are selected particularly carefully.

The absence of anthropogenic infrastructure was moderately important for roost site selection but was unimportant for the differentiation between night and day locations. Pre-breeding eagles likely avoided human infrastructure, much like adult golden eagles in previous studies (Maynard et al., 2024; Sur et al., 2019). In addition to the direct avoidance effects of human infrastructure, food availability may also be reduced, as prey occurrence is often negatively impacted by human presence (McLeod et al., 2002; Meisingset et al., 2022).

Although the territory border regions likely offer inferior living conditions compared to central territory habitats (Oro, 2008; Penteriani et al., 2011), pre-breeders showed a high survival rate throughout the first years after emigration in our study population (own unpublished data). This suggests that they can to some extent compensate for the suboptimal conditions, potentially by using space at a larger spatial scale than territory holders (Delgado et al., 2009; Rohner, 1997). Not being site-bound results in a larger spatiotemporal flexibility which enables pre-breeders to track ephemeral resources and quickly respond to changing habitat conditions (Stillman et al., 2022). Moreover, subordinate individuals may still access resources in areas of high competition during short-term foraging trips (Adams, 2001; Davies & Houston, 1981). We therefore suggest that pre-breeders rapidly become proficient at navigating the territorial challenges in a saturated population. However, the limited space likely increases competition between pre-breeders and contributes to the long time before they can recruit into dense populations. Individual differences in the ability to deal with such social interactions might be key for understanding the differences in the pre-breeders' future recruitment success (Chapter II and III; Bruinzeel & Van De Pol, 2004).

Movements of pre-breeding golden eagles can be segmented into alternating periods of encampment, in which temporary home-ranging behaviour is shown, and periods of exploration in which large-scale exploration movements are performed (Chapter III). Within the general avoidance of roost site selection of areas in proximity to core areas of territories, we showed that roost sites in encampment differed in habitat from roost sites during exploration. Roost sites that were further away from territory centres, but marginally deeper inside territories, were more likely to be used during periods of encampment compared to periods of exploration. This pattern suggests that pre-breeders prefer habitats for temporary home-ranging behaviour within territories where the trade-off between good habitat quality and limited exposure to territorial aggression is maximised. Conversely, roost sites during exploration behaviour were mainly along territory boundaries. Thus, pre-breeders likely can remain in patches because some sections of territories are too costly to be permanently defended by residents (Carrete et al., 2006; Giuggioli et al., 2011; Jenny, 1992). Undefended territory sections might particularly occur in large or topographically structured territories, where parts cannot be surveyed or at places where resource availability is comparatively lower than in other parts of the territory (Ewald et al., 1980). Thus, encampment of pre-breeders seems to occur in peripheral areas where pre-breeders are tolerated because the costs associated with territory defence outweigh the benefits (Holbrook & Schmitt, 1988; Penteriani et al., 2011). Such areas might have an important function as refuges for pre-breeders to rest and recover from permanent territorial interactions (Ewald et al., 1980).

During exploration, it appears crucial for pre-breeders to have access to habitats that offer concealment and quick escape routes. We found that pre-breeders selected habitats with higher forest cover and higher elevation during exploration compared to encampment. Forested areas likely provide enhanced concealment from territory holders and might not be fiercely defended by residents, allowing juveniles to remain undetected while still maintaining access to profitable resources and information within territories, as has been shown in predator-prey systems (Holbrook & Schmitt, 1988; Signorell et al., 2010). By roosting at high elevations that offer suitable uplift conditions (Scacco et al., 2019), pre-breeders have rapid access to orographic uplifts to swiftly gain altitude, cross ridge lines, and move into adjacent valleys when detected by residents. In contrast, during encampment, the generally lower levels of aggression from conspecifics prevailing likely allow for roosting in open habitats without the immediate need to have nearby forests for concealment. The variation in roosting habitat preferences mirrors the differential use of the limited space during the two movement phases and highlights the behavioural adjustments that are necessary for pre-breeding golden eagles to balance the trade-offs between safety and foraging efficiency.

Our findings indicate that patches where pre-breeders can show encampment behaviour are rare in a dense social system, because such patches need to fulfil both a low exposure to agonistic behaviours and highly suitable foraging habitat. Pre-breeders only spend one third of their time during transience in encampment (Chapter III), and although such encampment patches might be an important resource, there may be large individual differences in what constitutes ideal habitat for an individual to remain in (Lent & Fike, 2003). Our model explaining the differences between roosts selected during encampment and exploration had limited between-individual predictability, indicating that pre-breeders showed large individual differences in their selection, a pattern that has been observed in different systems as well (McCabe et al., 2021; Trevail et al., 2021). Because the within-individual predictability of roost sites during encampment was slightly higher, we speculate that each individual repeatedly used a specific set of encampment patches throughout the pre-breeding period, as shown in different studies (Port et al., 2017). The finding that some exemplary patches where our tracked eagles remained during encampment overlapped with regions Haller (1996) described as temporary home ranges of pre-breeders indicates long-term consistency of these pre-breeder encampment patches. As golden eagles like many other bird species rely on social information, the presence of pre-breeders could give away clues for other pre-breeders to gather there. Benefits from clustering together can include a dilution effect of aggressive interaction pressure by safety in numbers (Chapman & Kramer, 1996; Lehtonen & Jaatinen, 2016) or a share of information (Fletcher et al., 2006). Whether and how space is shared between individuals can only be speculated about, as the number of pre-breeders we tagged was small compared to the whole pre-breeder population. Even though individual variability in roost site selection was high, likely affected by individual phenotypic variation (Chapter III), some basic parameters of safety and food availability appeared to be selected in most individuals and therefore space-use patterns could persist for decades.

Conclusion

In dense populations, the social environment of territoriality imposes strong limitations on the accessibility of habitat to pre-breeders. Navigating this limited space likely contributes to the emergence or persistence of specific habitat use, where pre-breeding eagles can only remain for an extended period, ranging from days up to a few weeks (Chapter III), in areas where agonistic pressure is low. By remaining integrated in the population pre-breeders can swiftly fill emerging gaps in the territorial system, thus stabilising population fluctuations (Hunt, 1998). On the other hand, they also directly affect the breeding population by evoking stress and deterring resources in terms of energy and time from residents, often lowering breeding success (Jenny, 1992; Penteriani et al., 2005). We thus propose that the social environment has an underestimated but crucial role in affecting range use during natal dispersal, thereby driving population level processes of recruitment and juvenile survival. Understanding the spatial structure of different demographic groups of a population can further help guiding conservation actions and management decisions to protect the often-overlooked pre-breeders.

5.6 Supporting information

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Competing interests

We declare we have no competing interests.

Declaration of originality

We declare we came up with the research question and have written the full text ourselves.

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Ethics statement

Catching, ringing and tagging were conducted under the licences of the responsible institutions in the different countries and disturbance was kept to a minimum (CH: Food Safety and Veterinary Office Grisons, permit no. GR 2017_06, GR 2018_05E, GR 2019_03E, GR/08/2021, and the Federal Office for the Environment, licence no. TV201903E; DE: birds were handled, tagged and ringed under the permission issued by the government of Oberbayern (2532.Vet_02-16-88 and 2532.Vet_02-20-86); IT: the permissions for handling, tagging and marking were obtained from autonomous region of South Tyrol (Dekret 12257/2018 and Dekret 8788/2020), as well as from the Regione Lombardia and Sondrio Province for ringing and tagging in Lombardia and South Tyrol by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale) with the Richiesta di autorizzazione alla cattura di fauna selvatica per scopi scientifici (l.r. 26/93).

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5.8 Supplementary material

Table S1. List and description of predictor variables used to explain overnight roost site selection of pre-breeding golden eagles during 2018 – 2024 in Switzerland. Represented is the mean relative importance and standard deviation for each predictor variable and model. We obtained landcover data from the Swiss Landuse Statistics (Federal Statistical Office) and topographical data from a Digital Elevation Model DEM (DHM25 © swisstopo).

Variable name	Description	Relative importance for roost site vs random absence site selection	Relative importance for roost site vs daytime site selection	Relative importance for roost site selection during encampment vs exploration
Social environment				
Distance to territory centre	Distance in meters between used/available locations and the nearest nest centroid	0.80 ± 0.03	0.48 ± 0.04	1.00 ± 0.00
Distance to territory border	Distance in meters between used/available locations and the nearest territory boarder	0.61 ± 0.03	0.58 ± 0.04	0.70 ± 0.04
Landcover type				
Open vegetation	proportion of a 250 m radius covered by short vegetation including the categories 45-49 and 64-67	0.55 ± 0.02	0.70 ±0.03	0.51 ± 0.02
	proportion of a 1’500 m radius covered by short vegetation including the categories 45-49 and 64-67	0.65 ± 0.02	0.71 ± 0.04	0.79 ± 0.04
Forest	proportion of a 250 m radius covered by shrubs and trees	0.56 ± 0.02	1.00 ± 0.00	0.47 ± 0.02

		including the categories 50-60			
		proportion of a 1’500 m radius covered by shrubs and trees including the categories 50-60	0.55 ± 0.53	0.63 ± 0.04	0.92 ± 0.05
	Unvegetated	proportion of a 250 m radius without vegetation including the categories 69-72	0.48 ± 0.02	0.64 ± 0.03	0.56 ± 0.03
		proportion of a 1’500 m radius without vegetation including the categories 69-72	0.57 ± 0.03	0.68 ± 0.03	0.77 ± 0.04
	Anthropogenic landscape	proportion of a 250 m radius covered by anthropogenic infrastructure including the categories 1-44 and 68	0.42 ± 0.02	0.30 ± 0.04	0.14 ± 0.02
		proportion of a 1’500 m radius covered by anthropogenic infrastructure including the categories 1-44 and 68	0.57 ± 0.02	0.57 ± 0.03	0.81 ± 0.04
Topography					
	Elevation	Meters above sea level extracted from a 100x100 m resolution	0.55 ± 0.03	0.82 ± 0.05	0.80 ± 0.04
	Slope	Incline/steepness of a slope measured in degrees diverging from the horizon (0-90) derived from a 100 x100 m resolution	1.00 ± 0.00	0.91 ± 0.05	0.47 ± 0.03
	Territory Ruggedness Index TRI	Mean of the absolute differences between the elevation value of a cell with a 100x100 m resolution and the value of its 8	0.68 ± 0.02	0.75 ± 0.04	0.54 ± 0.04

	surrounding cells (Riley et al., 1999)			
Northness	Converted aspect (degrees 0-360) to radians using a 100 x100 m resolution cell grid with values between 1 (north exposition) and -1 (south exposition) using the formula cos(aspect*pi/180) derived from 100x100 m resolution	0.42 ± 0.02	0.68 ±0.05	0.54 ± 0.04
Eastness	Converted aspect (degrees 0-360) to radians using a 100 x100 m resolution cell grid with values between 1 (east exposition) and -1 (west exposition) using the formula sin(aspect*pi/180) derived from 100x100 m resolution	0.33 ± 0.02	0.59 ± 0.04	0.60 ± 0.05

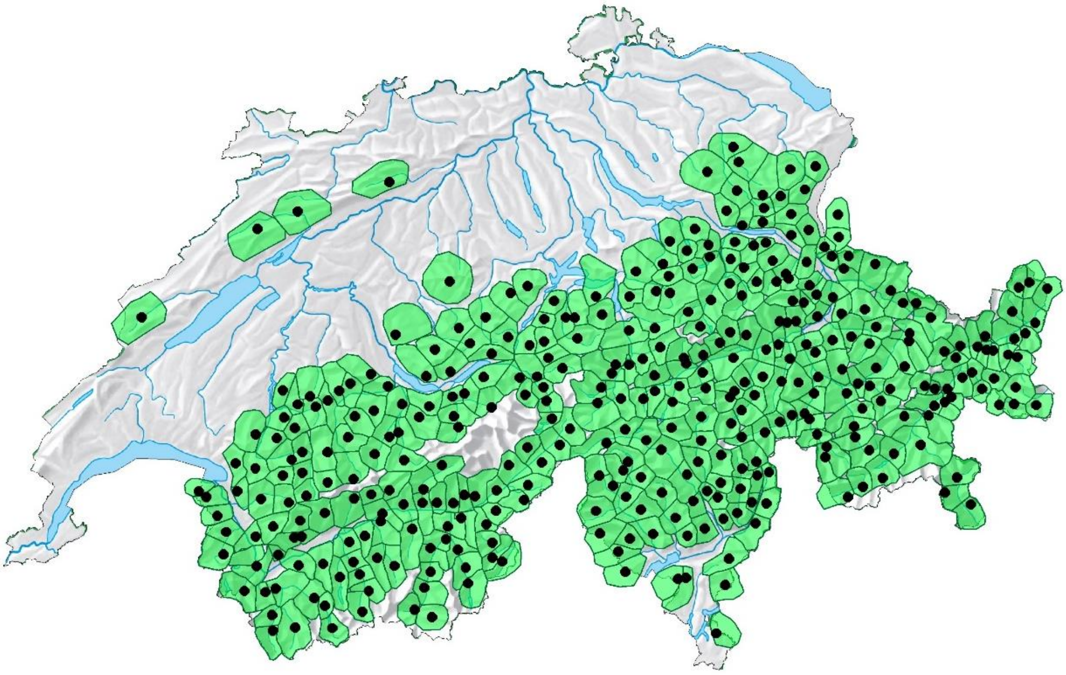
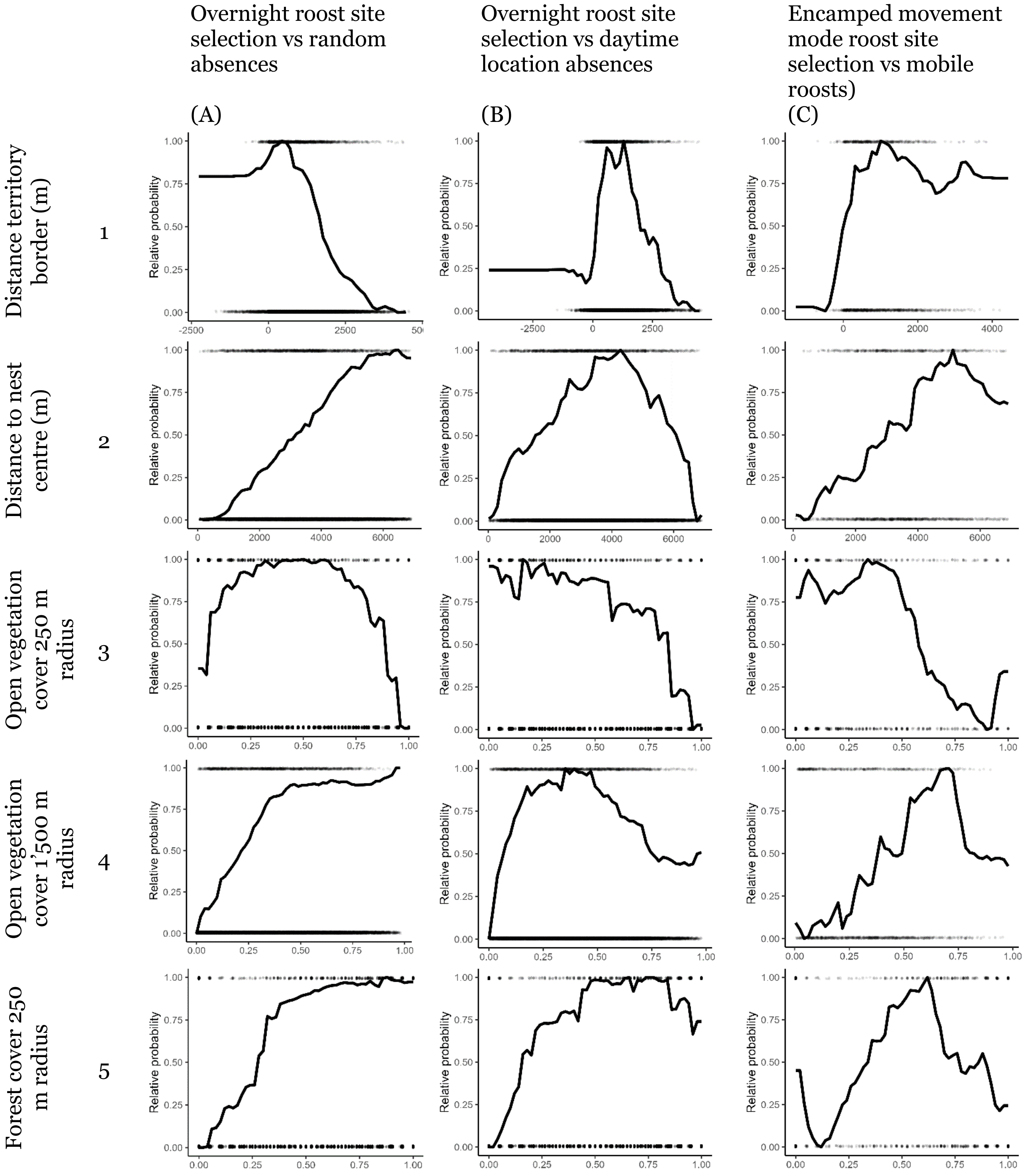
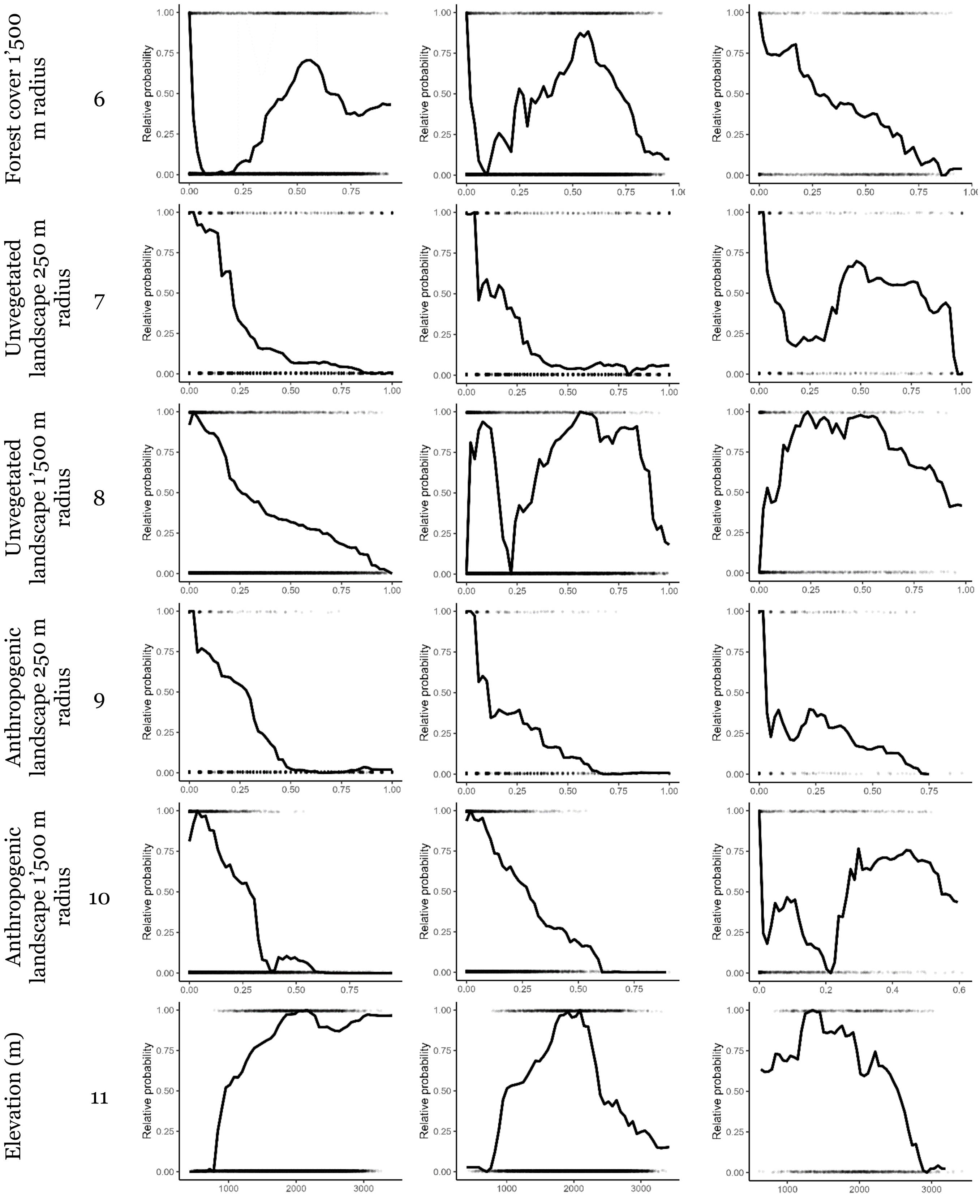


Figure S1. Golden Eagle territories in Switzerland in 2023 (cf. Jenny 2024). Territory boundaries were determined using field observations of territorial behaviour and topographical information. Nest centroids are indicated as black points. Source: Swiss Ornithological Institute; Base map: swisstopo.


Overnight roost site selection vs random absences
Overnight roost site selection vs daytime location absences
Encamped movement mode roost site selection vs mobile roosts)
(A)
(B)
(C)
Distance territory border (m)
1
Distance to nest centre (m)
2
Open vegetation cover 250 m radius
3
Open vegetation cover 1'500 m radius
4
Forest cover 250 m radius
5
Relative probability
0.00
0.25
0.50
0.75
1.00
-2500
0
2500
2000
4000
6000


Forest cover 1'500 m radius
6
Unvegetated landscape 250 m radius
7
Unvegetated landscape 1'500 m radius
8
Anthropogenic landscape 250 m radius
9
Anthropogenic landscape 1'500 m radius
10
Elevation (m)
11
Relative probability
0.00
0.25
0.50
0.75
1.00
0.0
0.2
0.4
0.6
1000
2000
3000

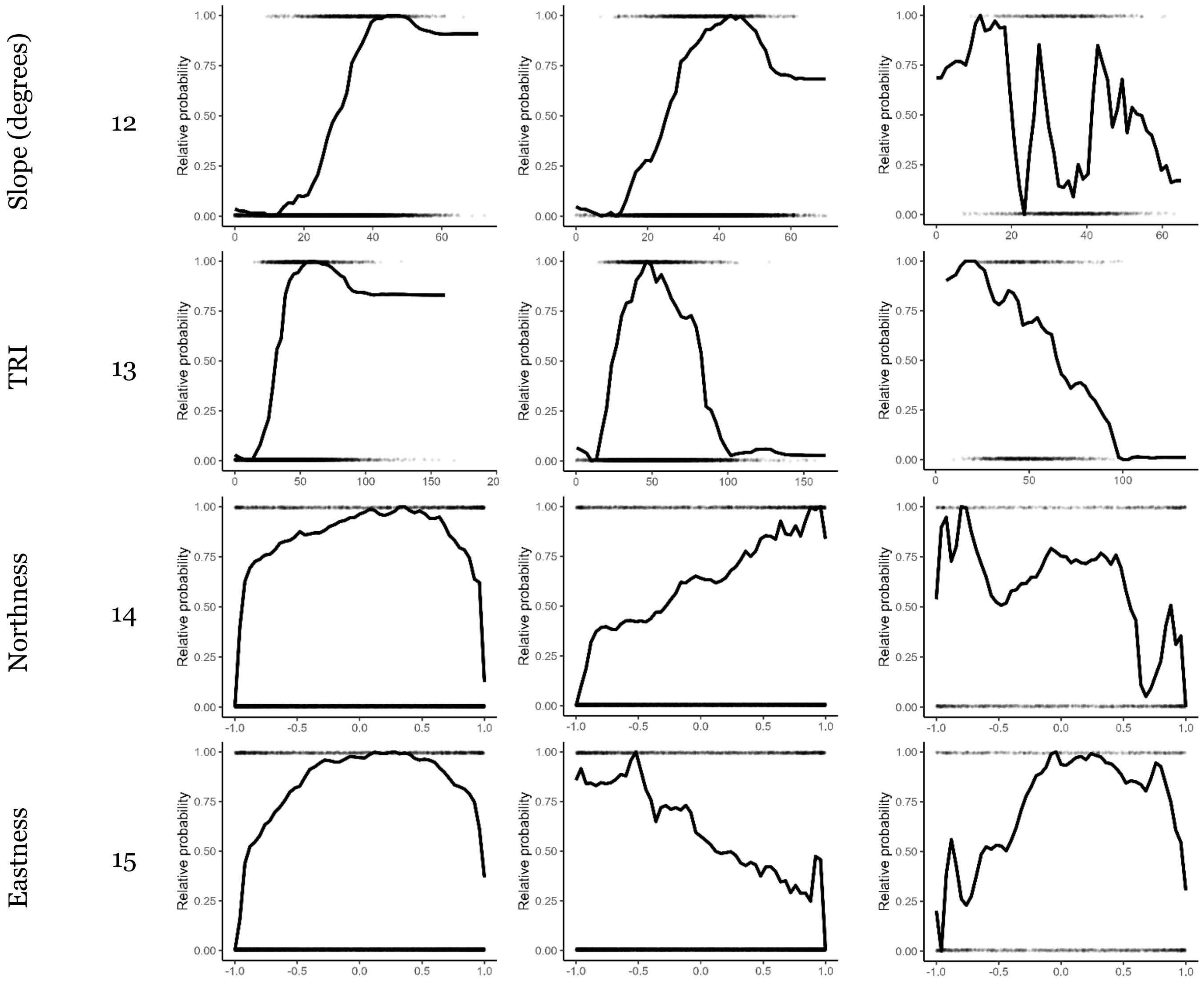


Figure S2. Matrix of plots illustrating the relationships between models and variables. Partial effect plots representing relative probability of selecting (A) a roost site vs a random site, (B) a roost site vs a daytime location, or (C) a roost site during encampment vs a roost site during exploration. We derived the relative partial effect of each predictor variable over the range of observed values (n = 200 per variable) while all other variables were held at their means and rescaled the predictions between 0 and 1 between the minimum and maximum value of each prediction for comparison. We ordered the partial effect plots following the order of table S1.: (1-2) social environment variables, (3-10) landcover variables, (11-15) topographical variables.

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6. General Discussion

Illustration: Lara Gross

> "If I seem to wander, if I seem to stray,
> remember that true stories
> seldom take the straightest way"
> — Patrick Rothfuss, The Name of the Wind

In my dissertation I investigated phenotypic variation throughout different life-history stages and linked them to early-life conditions. I uncovered inter- and intra-individual phenotypic patterns of pre-breeders in a saturated population of golden eagles. Specifically, I addressed the following questions: (1) How do early-life conditions shape behavioural phenotypes and how do these phenotypes affect pre-emigration excursion behaviour and emigration timing? (2) How do early-life flight behaviour and food conditions affect emigration timing? (3) How does movement and space use develop during the transience period and what role do natal legacies play in shaping individual variation? (4) How does the social environment influence the habitat selection of juveniles throughout transience?

I identified significant individual differences in the movement and space-use of juvenile golden eagles which persisted across multiple life-history stages. I found that high activity levels in the nest allowed individuals to fledge early, and nestling activity correlated with activity and exploration behaviour during the post-fledging phase (**Chapter I**). High post-fledging activity, energy-efficient flight behaviour, and favourable food conditions in the post-fledging period subsequently allowed individuals to emigrate early (**Chapters I and II**), indicating a relationship between favourable early-life conditions and early emigration timing. Individuals which emigrated early were more mobile and exploratory during the transience phase than late emigrating conspecifics (**Chapter III**). In the saturated Alpine population, pre-breeding golden eagles avoided areas near existing territory centres (**Chapter IV**) which likely has considerable effects on the space pre-breeders have access to. Together, the results of my thesis show that the natal environment is a strong determinant of individual behaviour throughout multiple life-history stages, and this has the potential to govern the process of successful recruitment into the breeding population.

Emergence of behavioural phenotypic specialisation

Through examining different life-history stages—within the nest, post-fledging, and transience periods—I found indications that golden eagles do not only vary in their behavioural expression in one life-history stage but that there are also (1) correlations between different behaviour phenotypes within a life history stage, and (2) correlations between behaviours (or sets of behavioural phenotypes) across life-history stages. For example, juveniles that were more active in the nest also maintained higher activity levels post-fledging, associated with more exploratory foray flights (**Chapter I**). Similarly, individuals that were more efficient in cost-effective flight emigrated at a younger age and displayed greater mobility during the transient phase (**Chapters II – III**). These findings suggest that while the specific behavioural phenotypes expressed vary across different life-history stages, the different sets of stage-specific phenotypes might be strongly correlated. Golden eagles therefore vary across a continuum of behavioural expression, ranging from an active-explorative to a passive-inert phenotype. This continuum might even be equivalent to the known behavioural syndrome (i.e. a suite of linked behavioural phenotypes that are consistently expressed together (Clobert et al., 2009; Sih et al., 2004), spanning from bold to shy (Dingemanse et al., 2010). For instance, shy individuals are often less active, less exploratory, and more submissive in interactions with conspecifics compared to bolder conspecifics (Sih et al., 2004). My findings thus indicate behavioural correlations across contexts and time that give rise to life-long behavioural syndromes, which could ultimately also shape dispersal syndromes (i.e. a suit morphological, behavioural, and/or life-history traits associated with dispersal (Clobert et al., 2012; Cote et al., 2017).

Fitness effects of behavioural phenotypes

The correlation between favourable food conditions, high body condition, and a more active-explorative phenotype (**Chapters I and II**) leads me to conclude that individuals with a more pronounced active-explorative phenotype might profit from life-long fitness benefits. The advantages acquired during early-life development might give juveniles persistent competitive advantages through improved cognitive skills (De Rooij et al., 2010), learning abilities (Brust et al., 2014) and body condition (Perrig et al., 2014), that culminate in an earlier timing of emigration. Benefits acquired during favourable conditions experienced early in life can often never be attain by later-emigrating peers (Van de Pol et al., 2006). Thus, early emigration timing could signal high quality individuals. This is in line with findings of previous studies. For instance, in densely populated seabird colonies, chicks that fledge earlier than their peers may secure better feeding grounds, leading to higher survival rates and improved physical condition (Lamb et al., 2016). Thus, favourable early-life conditions might give rise to behavioural syndromes which increase life-long fitness.

The competitive advantages juveniles may obtain by emigrating early could be linked to lower exposed to intra-specific competition until their later-emigrating peers enter the transient population. During the early stage of transience, individuals have little knowledge of the environment outside of the parental territory are thus naïve to their novel surroundings (Delgado et al., 2009). Being able to acquire knowledge without the juveniles from the same cohort around might allow early transients to monopolise and exploit resource rich areas. Indeed, in the first year of transience I found that early emigrating birds tend to remain in encampment areas longer than late emigrants (**Chapter III**). Although younger individuals are less competitive than older birds or adults, the reduced competition experienced during the early information-gathering period could provide a key advantage. However, I found indications that fitness might be considerably decreased for the few very early emigrating individuals. Direct observations of the small sample of individuals emigrating only a few weeks after fledging (n = 4) indicates that premature emigration can also be triggered by parental behaviour rather than juveniles' own decisions. One prematurely emigrating juvenile exhibited begging behaviour at other territories and died shortly after emigration. We suspected a change in the composition of the territorial pair in the natal territory prior to the juvenile emigration (pers. communication Fankhuser Thomas)—highlighting that premature dispersal can also have strong negative effects on survival. This example underscores that different mechanisms might be at play determining the timing of emigration ("parent-offspring-conflict" (Grüebler & Naef-Daenzer, 2008; Rotics et al., 2021; Trivers, 1974)). It would thus be crucial to examine the role of parental behaviour in future studies investigating emigration decisions. However, my results clearly show that the timing of emigration overall reflects early-life conditions and suggests that this metric could be a used as a proxy for differential individual quality.

Although I conducted my research in a saturated population, I am confident that the observed patterns of early emigration are not a consequence of this high population density, but rather that the same beneficial effects would also hold true in less dense populations. Early-life benefits and lifelong fitness consequences have been shown in multiple species, irrespective of conspecific context (Criscuolo et al., 2008; Jonsson & Jonsson, 2014; Rotics et al., 2021). Yet, in a high-density environment, resources are highly limiting and are insufficient to allow survival of all individuals, heightening the selective pressure compared to lower density environments. Thus, the consequences of individual strategies are likely more pronounced in high population densities. In less dense populations, later emigrating individuals might still show similar movement behaviour to early emigrating individuals during transience but acquire only the inferior, lower quality habitats rejected by their earlier peers, with ultimately also results in lower lifetime reproductive success. In high density populations, the consequences of individual differences are shown markedly, as uncompetitive individuals likely are unable to obtain a territory, thus never effectively dispersing (i.e., dispersal followed by successful reproduction). In contrast, at low densities even relative uncompetitive birds may successfully acquire a breeding territory, and so the consequences of their relative differences in the short-term may be less apparent and only become clear with an assessment of lifetime reproductive success of individuals.

Population expansion or population concentration?

Although the main Alpine range is close to saturation point, adjacent mountainous areas still hold significant potential for the establishment of new territories as suggested by Jenny (2024). However, the monitoring of golden eagle breeding pairs in Switzerland has shown that there have been hardly any new territories forming in a proximate mountain range over the course of the last decades (Knaus et al., 2018). My results suggest that despite the high density prevailing in the Alps, the alpine population is likely spreading very slowly, and I suggest two main reasons for this. First, juvenile eagles show strong philopatric behaviour by being strongly tied to the Alpine region, with very few instances of juveniles undertaking excursions across surrounding lowland areas (**Chapter III and IV**). The phenomenon of preferring habitats close to home, also referred to as natal habitat preference induction (NHPI), has been observed in multiple species (Davis & Stamps, 2004; Stamps & Swaisgood, 2007). Flatter terrain also provides poorer conditions for orographic uplift, and this could limit the ability of pre-breeders to explore such environments. Young golden eagles mainly rely on the easier to exploit orographic during the first years of life (Nourani et al., 2024). Second, social attraction may further delay the expansion of golden eagles into areas of lower population densities. Like many large soaring birds, golden eagles rely heavily on social information to locate food and suitable habitats, often orienting themselves based on the presence of other individuals (Cortés-Avizanda et al., 2014; Gil et al., 2018). This is also supported by my finding that encampment areas are spatially and temporally overlapping between pre-breeders (**Chapter IV**). The absence of socially-communicated information in these less populated areas might therefore reduce the likelihood of eagles establishing themselves in new regions, which could result in even heightened population concentration within the Alpine range.

Although typical territories within the Alpine range are around 77 km^2, the Alpine range has space for some more pairs, as evidenced by recently established micro-territories of areas as small as 9 km^2. (Jenny et al., 2024). Holding a large territory incurs considerable costs for territory holders, and the pressure of pre-breeders is likely to lead to smaller territory sizes, opening up more space for potential new territories (López-Sepulcre & Kokko, 2005). However, the extent to which a territory sizes could shrink remains an open question. Since encampment habitats do not appear to be converted into territories, they likely lack the resources necessary to support a breeding pair. Food availability is a clear factor limiting the establishment of new territories, however the availability of suitable breeding sites (Coudrain et al., 2010; Village, 1983) with favourable topographical conditions also plays a role (Jenny et al., 2024). A greater understanding of these factors limiting territory establishment is therefore critical to understanding which parts of the landscape hold the potential for new territory establishment and how the movement behaviours identified in this thesis could influence an individual's ability to access these areas.

Even though I anticipated that pre-breeding golden eagles were bound to the Alpine range, I expected a more extensive space use along the east-west axis of the Alpine range, or at least a higher degree of individual variability in distances covered during transience (Weston 2013). In a non-migratory golden eagle population in North

America, differential dispersal strategies were observed, with most juveniles remaining within approximately 100 km of the natal territory, while some individuals travelled distances exceeding 1'000 km (Poessel et al., 2022). I showed in **Chapter III** that the costs of remaining in this saturated population likely increase with time spent in transience, as juveniles became increasingly mobile as they aged. This trend was contradictory to assumptions that with increasing knowledge and experience individuals make more informed decisions that result in reduced, more targeted, movement (Brønnvik et al., 2024; Efrat et al., 2023). The increasing mobility was likely a consequence of the constant social pressure and agonistic encounters that become stronger with approaching sexual maturity.

Preliminary analysis for home range size and dispersal distance showed that pre-breeders remained within the proximity of their birthplace and did not explore large parts of the Alpine range. This pattern indicates that there are high costs associated with exploring new areas or, conversely, considerable benefits associated with remaining integrated in the breeding population. In densely populated areas, intense competition may limit the ability of juveniles to explore large areas of the Alpine realm due to constant pressure of territorial conflicts and limited space (Forero et al., 2002), which can inhibit exploration (Matthysen, 2005). Previous research supports the theory that the survival probability of juveniles decreases significantly with increasing distance from their natal territories in the first two years following dispersal (Murphy et al., 2017). Benefits of staying are likely associated with a deep knowledge about food resources (Wolf et al., 2009), breeding habitats which can increase their chances of acquiring territories (Stamps, 1987). These findings indicate that the advantages of known resource-rich areas are critical, and juveniles may tolerate highly competitive pressure to maintain access to these areas.

Conservation implications

Thanks to extensive conservation measures in the mid-19th century, the Alpine golden eagle population has recovered from less than 100 pairs (Glutz von Blotzheim, 1965; Jenny et al., 2024) and is now classified vulnerable rather than endangered (IUCN, 2024). Although direct persecution has diminished, anthropogenic pressure on nature is increasing across the Alps. Infrastructure in the alpine regions has developed substantially over recent decades, as has human use of these previously remote regions

(Salata, 2014). The decline in snow cover, a along with the expansion of roads and transport infrastructure such as cable cars, has made previously isolated and undisturbed habitats more accessible to tourist activities, thereby increasing wildlife disturbance (Peęksa & Ciach, 2015). Furthermore, the growing demand and transition to greener energy will result in the development of large-scale solar and wind energy parks in mountainous regions due to the high energy potentials (IEA, 2024; Kahl et al., 2019). Further, climate change and the abandonment of extensive Alpine pastures in rural areas are expected to threaten open vegetation habitats—the predominant feeding grounds of golden eagles—by facilitating shrub and forest encroachment (Anselmetto et al., 2024; Tasser et al., 2017).

My research provides insights into the requirements of juvenile golden eagles and highlights possibilities for their conservation. Up to now, conservation efforts of golden eagles have, however, mainly focused on adults and their nest sites. Preserving undisturbed nesting sites and territories is indeed crucial, as it allows adults to provide good early-life conditions to their offspring. However, I also advocate for the importance of undisturbed areas for pre-breeders in future conservation planning. First, my findings provide evidence that pre-breeders remain in the interstices of territories in far distance to nest sites (**Chapter IV**). Thus, critical habitats for pre-breeders may be at risk of development or destruction, as their ecological significance remains overlooked in conservation planning. Considering pre-breeder habitat is especially crucial, as those habitats seem to be persistent over time. Some of those areas which my results highlight as being important to pre-breeders under current conditions were highlighted almost 40 years ago for the same reasons (Haller, 1982, 1996). Haller's comprehensive study on the golden eagle population in the Engadine, a part of the Swiss Alps the core of my study area, exemplified sites where young eagles congregate. Current, continuing anthropogenic changes risk the loss not only of high-quality breeding areas but also of temporary settlement areas that are important for pre-breeders. This in turn may force pre-breeders to search for alternative habitats which are already rare. The increased confrontation with territory holders and anthropogenic infrastructure during the search for alternatives could increase pre-breeder mortality which could negatively affect population persistence. Indeed, increased pre-breeder mortality is particularly concerning, as the impact on population dynamics may only become apparent once populations are already in decline

(Penteriani et al., 2005, 2011). Future conservation efforts thus need to account for differences in the habitat quality of breeding territories and include strategies for the protection of areas of importance to pre-breeders.

Conclusion

By linking early-life conditions to emergent movement and behavioural patterns during natal dispersal, I showed in my dissertation that conditions during early life substantially affect behavioural phenotypic variation. This variation is likely perpetuated throughout successive life-history stages into adulthood. Without considering the correlation between favourable early-life conditions and the timing of emigration, I may have interpreted the increased mobility during the transient phase of early-emigrating individuals as disadvantageous, since previous literature often associates heightened mobility with reduced competitiveness in individuals. While I can still only hypothesise that early emigration timing and increased mobility during transience are indicators of high-quality individuals, the consistent patterns observed across a significant portion of the golden eagles' life-history trajectory leaves me with a strong degree of confidence in this interpretation. I advocate that integrative approaches for examining the emergence and persistence of behavioural phenotypes should be granted more emphasis in population-level studies. This will provide a better understanding of the mechanisms underlying fundamental processes such as recruitment and allow their effects upon the population dynamics of long-lived species to be understood.

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7. Acknowledgements

Illustration: Lara Gross

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8. Impressions

Figure 9.1. Recording individual characteristics during the tagging process. © Romano Salis

Figure 9.2. Reaching tagging locations often involved hiking through beautiful landscape early in the morning. © Julia Hatzl

Figure 9.3. The briefing of the team before each tagging event was routine. © Julia Hatzl

Figure 9.4. Tagging falconry golden eagles at the Adler-Arena Burd Landskron allowed us to collect behavioural observations simultaneous to accelerometer data. © Michel Schmidlin

Figure 9.5. Searching for the VHF-singal of an individual even in the middle of winter. © Julia Hatzl

Figure 9.6. When GPS and ACC data indicated that an individual died or a tag was lost we tried to rapidly reach the location and locate the tag using the VHF-signal. © Julia Hatzl

9. Curriculum Vitae

Full name: Julia Solveig Hatzl

Date of Birth: 24 February 1992

Nationality: Austria

Education

2019 – 2024 **Ph.D. – Ecology**

ETH Zurich and Swiss Ornithological Institute, Switzerland

Thesis title: “Tracking behavioural trajectories: early-life effects on natal dispersal patterns in golden eagles (*Aquila chrysaetos*)”

2014 – 2016 **Master of Science – Ecology and Evolution**

University of Zurich, Switzerland

Thesis title: “Parasites in a population of feral horses”

2010 – 2014 **Bachelor of Science – Biology**

University of Innsbruck, Austria

Thesis title: “Migration pattern of *Bufo bufo* and *Rana temporaria* in the frontier area of Mauren-Tosters (Liechtenstein-Vorarlberg).”

Practical Experience

2018 – 2019 Internship at the Swiss Ornithological Institute Sempach, Switzerland

Behavioural observation of GPS-tagged Golden Eagles (*Aquila chrysaetos*) and monitoring of breeding pairs.

2017 – 2018 Internship at naturschutz.ch, Switzerland

Science communication

2016 – 2018 Teaching position at Life Science Learning Centre LSLC, Switzerland

Environmental education

2016 – 2017 Internship at Pro Natura Graubünden, Switzerland

Conferences and Presentations

Scientific conference contributions

2024	DO-G Tagung, Austria, Vienna – Oral presentation
2024	International Bio-Logging Science Symposium, Tokyo, Japan – Coauthor Poster
2024	Centennial Symposium Swiss Ornithological Institute, Sempach, Switzerland – Oral presentation
2022	International Ornithological Conference, Durban, South Africa (online only) – Oral presentation
2022	International Society for Behavioural Ecology, Stockholm, Schweden – Oral presentation
2022	Lifescience PhD Ecology Program Biennal Symposium, Zurich, Switzerland – Poster
2019	European Ornithological Conference, Cluj, Romania – Poster

Non scientific presentations

2024	Junge Steinadler im Fokus: Einblick in 7 Jahre Forschung – Ornithologische Gesellschaft Graubünden, Switzerland
2023	J. Hatzl: Steinadler – König der Lüfte – Ornithologischer Verein Basel, Switzerland
2022	Steinadler – König der Lüfte – Milan Vogelschutz Biel, Switzerland

Publications peer reviewed

Published

Nourani, E., Faure, L., Brønnvik, H., Scacco, M., Bassi, E., Fiedler, W., Grüebler, M. U., **Hatzl, J.S.**, Jenny, D., Roverselli, A., Sumasgutner, P., Tschumi, M., Wikelski, M., & Safi, K. (2024). Developmental stage determines the realized energy landscape for a flight specialist. *ELife*, *13*. https://doi.org/10.7554/eLife.98818.1

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Outreach articles not peer reviewed

Book chapter

Jenny, D., Denis, S., Cruickshank, S. S., Tschumi, M., **Hatzl, J.,** & Haller, H. (2024). The Golden Eagle in Switzerland. In J. Bautista & D. H. Ellis (Eds.), *The Golden Eagle Around the World: A Monograph on a Holarctic Raptor*. Hancock House Publishers.

Articles

J. Hatzl, D. Jenny, K. Safi: Anspruchsvoller Start ins Leben (2024). Ornis

D. Jenny, K. Safi, **J. Hatzl**: Im Fokus der Forschung: Junge Steinadler (2022). Der Falke

D. Jenny, **J. Hatzl**: Jungen Steinadlern auf der Spur (2020). Avinews

Video and Audio Media

J. Hatzl: Der Steinadler (2022). Schweizerische Vogelwarte Sempach — Podcast

J. Hatzl: Wandern mit dem Steinadler (2018). Post — Video

Scientific Collaborations and Supervision

2024	Collaboration PhD student, Konrad Lorenz Research Center (KLF), Grünau/Almtal
2024	Co-supervision M.Sc. student, Swiss Ornithological Institute, Switzerland
2023	Collaboration M.Sc. student, Max Planck Institute for Animal Behaviour, Konstanz, Germany
2021	Collaboration B.Sc. student, University of Munich, Munich, Germany
2021	Co-supervision M.Sc. student, Swiss Ornithological Institute, Switzerland