UNIL | Université de Lausanne

Unicentre
CH-1015 Lausanne
http://serval.unil.ch

Year : 2023

The non-breeding period of the Western barn owl (Tyto alba): Habitat selection, activity patterns and fitness

Bühler Roman

Bühler Roman, 2023, The non-breeding period of the Western barn owl (Tyto alba): Habitat selection, activity patterns and fitness

Originally published at : Thesis, University of Lausanne

Posted at the University of Lausanne Open Archive http://serval.unil.ch
Document URN : urn:nbn:ch:serval-BIB_354C8834608C4

Droits d'auteur
L'Université de Lausanne attire expressément l'attention des utilisateurs sur le fait que tous les documents publiés dans l'Archive SERVAL sont protégés par le droit d'auteur, conformément à la loi fédérale sur le droit d'auteur et les droits voisins (LDA). A ce titre, il est indispensable d'obtenir le consentement préalable de l'auteur et/ou de l'éditeur avant toute utilisation d'une oeuvre ou d'une partie d'une oeuvre ne relevant pas d'une utilisation à des fins personnelles au sens de la LDA (art. 19, al. 1 lettre a). A défaut, tout contrevenant s'expose aux sanctions prévues par cette loi. Nous déclinons toute responsabilité en la matière.

Copyright
The University of Lausanne expressly draws the attention of users to the fact that all documents published in the SERVAL Archive are protected by copyright in accordance with federal law on copyright and similar rights (LDA). Accordingly it is indispensable to obtain prior consent from the author and/or publisher before any use of a work or part of a work for purposes other than personal use within the meaning of LDA (art. 19, para. 1 letter a). Failure to do so will expose offenders to the sanctions laid down by this law. We accept no liability in this respect.

UNIL | Université de Lausanne

Faculté de biologie
et de médecine

Department of Ecology and Evolution

The non-breeding period of the Western barn owl (*Tyto alba*): Habitat selection, activity patterns and fitness

Doctoral thesis in life sciences (PhD)

presented to
Faculty of Biology and Medicine
of the University of Lausanne

by

Roman Bühler

Master of science in Ecology, University of Bern

Jury

Prof. Dr. Olivier Michielin, President
Prof. Dr. Alexandre Roulin, Thesis supervisor
Dr. Bettina Almasi, Thesis co-supervisor
Dr. Martin Grübler, Expert
Dr. Kamran Safi, Expert

Lausanne 2023

UNIL | Université de Lausanne

Faculté de biologie
et de médecine

Department of Ecology and Evolution

The non-breeding period of the Western barn owl (*Tyto alba*): Habitat selection, activity patterns and fitness

Doctoral thesis in life sciences (PhD)

presented to
Faculty of Biology and Medicine
of the University of Lausanne

by

Roman Bühler

Master of science in Ecology, University of Bern

Jury

Prof. Dr. Olivier Michielin, President
Prof. Dr. Alexandre Roulin, Thesis supervisor
Dr. Bettina Almasi, Thesis co-supervisor
Dr. Martin Grübler, Expert
Dr. Kamran Safi, Expert

Lausanne 2023

UNIL | Université de Lausanne
Faculté de biologie
et de médecine

Ecole Doctorale
Doctorat ès sciences de la vie

Imprimatur

Vu le rapport présenté par le jury d'examen, composé de

Président·e	Monsieur	Prof.	Olivier	**Michielin**
Directeur·trice de thèse	Monsieur	Prof.	Alexandre	**Roulin**
Co-directeur·trice	Madame	Dre	Bettina	**Almasi**
Expert·e·s	Monsieur	Dr	Martin	**Grübler**
	Monsieur	Dr	Kamran	**Safi**

le Conseil de Faculté autorise l'impression de la thèse de

Roman Bühler

Master of Science in Ecology and evolution, Université de Berne, Suisse

intitulée

The non-breeding period of the Western barn owl (*Tyto alba*): Habitat selection, activity patterns and fitness

Lausanne, le 24 novembre 2023

pour le Doyen
de la Faculté de biologie et de médecine

Prof. Olivier Michielin


1.'23

Content:

Acknowledgements

Undoubtedly, my PhD journey had its fair share of ups and downs. However, there was one constant through my thesis: my supervisor's stoic calmness. It is not everyone's cup of tea to be abruptly interrupted during their evening peace at 10 p.m. with news that their PhD student has rendered two assays on blood plasma samples useless. Thus, I extend a heartfelt thank you to Dr. Bettina Almasi for her tireless support whenever and wherever it was needed.

I would also like to express my deep gratitude to the "father" of the barn owl study population, Prof. Dr. Alexandre Roulin, who was always available to offer guidance, advice, and valuable input on the study design. Additionally, I extend my thanks to all the people from the University of Lausanne who contributed to the project, as their collective efforts were immensely important for its success.

I am sincerely grateful to the committee members who chaired and reviewed my thesis. Many thanks to the committee chair, Prof. Dr. Olivier Michielin, as well as the external reviewers, Dr. Kamran Safi and Dr. Martin Grüebler, for dedicating their time to reading and discussing my manuscript. I also want to acknowledge the valuable contributions of the internal committee members from the Swiss Ornithological Institute: Dr. Susi Jenni-Eiermann, Prof. Dr. Lukas Jenni, and Dr. Martin Grübler, who played significant roles in the development of the project.

I cannot express enough gratitude to all the field assistants who have been by my side through both good and challenging times. From stuck vehicles to nest boxes filled with decaying mice and owl droppings everywhere, they have endured numerous trials. Sitting in a pitch-dark barn for up to five hours, surrounded by blood-thirsty martens, is not a task that everyone can handle, and only the best of the best were able to work on this project. Their contributions were invaluable, as were those of the master students who assisted in data collection.

Furthermore, I want to extend my appreciation to the farmers within the study region, whose support and cooperation made the project possible in various ways.

I don't believe my parents ever envisioned raising a biologist, but here we are, 34 years later! The enriched environment provided during my early developmental phase has undoubtedly played a significant role in reaching this point. While my mother primarily fostered the development of my soft skills, my father imparted a different set of

practical skills, such as carpentry and automotive mechanics. While these specific skills may not have directly applied to my career as a biologist, the general craftsmanship skills have proven to be invaluable during fieldwork on numerous occasions. It is fair to say that I owe my current position and achievements to the unwavering support of my parents. They have made it possible for me to pursue this path, and their unconditional support is not something to be taken for granted. It is truly a tremendous privilege. Thank you for believing in me and providing the foundation for my journey as a biologist.

Finally, I would like to extend my sincere appreciation and gratitude to my fiancée, Chantal, for her unwavering support during this demanding period. Adapting to being unexpectedly awakened in the middle of the night by my French phone conversations was undoubtedly a challenge. Enduring the constant complaining and whining required considerable patience and resilience. Despite these difficulties, Chantal's love, encouragement, and steadfast presence by my side have been immeasurable. I am truly grateful for her unwavering support and understanding throughout this intense time.

Summary

Although the non-breeding period accounts for more than half of an animal's annual cycle, it is relatively little studied. Recent technological advancements have facilitated the tracking of animals during periods when direct observation is not feasible. By obtaining information on an individual's location and movement, one is nowadays able to address a wide range of ecological questions related to animals' behaviour and ecology during the non-breeding periods.

In the first chapter I quantified the habitat composition and the prey availability within the non-breeding home ranges of barn owls. Prey availability during the non-breeding period shows a patchier distribution compared to the breeding period. These changes in prey distribution then result in a grassland-oriented habitat selection. Furthermore, my data also indicate that semi natural habitats, such as wildflower areas and hedges, as well as field margins serve as important refuge and source of small mammals within the agricultural landscape.

In my second chapter I shed a first light on activity patterns of barn owls during the non-breeding period. My data suggests that barn owls exhibit a specific nightly movement pattern, suggesting an adaptation to the activity patterns of their prey. In addition, barn owls adapt different hunting strategies depending on the prey activity density in different habitat types. Furthermore, for individuals of each sex, the response to prey activity density is correlated with their individual pheomelanin-based colouration, possibly reflecting their prey species preference.

In the third chapter I investigated how environmental and individual conditions among different timepoints within the life cycle affect survival and reproduction of barn owls. Differences in the reproductive roles of males and females can lead to divergent impacts of environmental conditions and individual quality on fitness at different time points. Early-breeding males occupying prey-rich areas, are related to greater reproductive success but seem to face higher reproductive costs. Favourable post-breeding environmental conditions appear to be able to mitigate these effects in males. Conversely, female owls appear to benefit from early breeding and high food availability during the breeding period, leading to enhanced reproductive success while maintaining body condition. Unlike males, females do not seem to exhibit a clear trade-off between reproductive success and survival.

Résumé

Malgré qu'elle occupe plus de la moitié du cycle annuel des animaux, la période en dehors de la saison de reproduction reste relativement peu étudiée. Les avancées technologiques récentes ont facilité le suivi des animaux pendant les périodes où l'observation directe n'est pas possible. En obtenant des informations sur la localisation et les déplacements d'un individu, on est désormais capable de traiter un large éventail de questions écologiques liées au comportement et à l'écologie des animaux pendant les périodes de non-reproduction.

Dans le premier chapitre, j'ai quantifié la composition de l'habitat et la disponibilité des proies au sein des territoires des Effraies des clochers en dehors de la saison de reproduction. La disponibilité des proies pendant cette période présente une distribution plus morcelée par rapport à la période de reproduction. Ces changements dans la distribution des proies se traduisent ensuite par une sélection d'habitat orientée vers les prairies. De plus, je suggère que les habitats semi-naturels, tels que les zones de prairie fleurie et les haies, ainsi que les bordures de champs, servent de refuge important et de source de petits mammifères au sein du paysage agricole.

Dans le deuxième chapitre, j'ai mis en lumière les patterns d'activité des Effraies en dehors de la saison de reproduction. J'ai indiqué que les Effraies présentent un pattern de déplacement nocturne, probablement due à une activité accrue de leurs proies. Mes données suggèrent que les Effraies adaptent leurs stratégies de chasse en fonction de la densité d'activité des proies dans certains types d'habitats. De plus, pour les individus des deux sexes, la réaction à la densité d'activité des proies est corrélée à leur coloration basée sur la pheomélanine, reflétant peut-être leur préférence pour les espèces de proies.

Dans le troisième chapitre, j'ai étudié comment les conditions environnementales et individuelles à différents moments du cycle de vie affectent la survie et la reproduction des Effraies. Les différences dans les rôles reproducteurs des mâles et des femelles peuvent conduire à des impacts divergents des conditions environnementales et de la qualité individuelle sur le fitness à différents moments. Des mâles qui se reproduisent tôt et occupent des zones riches en proies sont associés à un plus grand succès reproducteur mais semblent faire face à des coûts de reproduction plus élevés. Les conditions environnementales favorables après la reproduction peuvent atténuer ces effets chez les mâles. En revanche, les femelles Effraies semblent bénéficier d'une reproduction précoce et d'une forte disponibilité de nourriture pendant la période de reproduction, ce qui

conduit un succès reproductif accru tout en maintenant leur état corporel. Contrairement aux mâles, les femelles ne semblent pas présenter de compromis clair entre le succès reproducteur et la survie.

General Introduction

The non-breeding period

The breeding period is a pivotal stage in the life cycle of animals that significantly influence population dynamics and as a result has been extensively researched, with numerous studies focusing on various aspects of animal reproduction. However, there is a noticeable bias towards research conducted during the breeding period compared to the non-breeding period [1]. This disparity in research attention creates a substantial knowledge gap within the annual life cycle of a species especially since the breeding period often covers a relatively short period of time. With the non-breeding period receiving less scientific exploration, the understanding of a species' overall life cycle often remains incomplete [1].

Recent studies have demonstrated that although breeding and non-breeding periods are typically distinct in terms of timing and location, they can still influence each other [2]. The impact of the non-breeding period on the fitness of animals has been well established for various mammal and bird species [3–7]. Thus, to attain a comprehensive understanding of individual habitat selection, behaviour and fitness in animals, it is essential to investigate the non-breeding period alongside the breeding period, ensuring a holistic view of animal life cycles.

One reason for the prevailing bias towards studies conducted during breeding periods is the increased accessibility of many study species during this period [1]. During breeding, animals tend to be tied to a particular location, making it easier to capture and monitor them. In contrast, during the non-breeding period, animals may have greater spatial freedom or even embark on long-distance migrations. Nonetheless, recent advancements in tracking technology have revolutionized the field, allowing for the monitoring of animals over extended periods and across vast distances [8]. These technological advancements have facilitated the collection of data on animal movements and behaviours during non-breeding periods, independent of human observation. As a result, valuable insights into the behaviour of migratory, nomadic, or resident species have been unveiled, contributing to a more comprehensive understanding of animal ecology.

Habitat selection

In heterogeneous landscapes, diverse habitats with varying resource availability exist. Animals are expected to preferentially choose habitats that provide the essential resources, leading to enhanced fitness levels. Consequently, animals are ideally inclined to select specific habitats over others to maximize their fitness potential [9]. But which habitat type best suits the needs of an animal changes with period specific requirements and availability of certain resources within the habitats [10–15]. For example, during the breeding season, animals may prioritize habitats which provide specific resources such as nesting sites or high-energy food, whereas some of these resources may become less important or available in other periods of the life cycle and habitat selection changes accordingly.

Habitat selection is therefore a complex process that can be examined at different spatial and temporal scales. Spatial scales of habitat selection analysis include selection of the geographical range by species (first order), home range within the species range (second order), habitat types within the home range (third order), or even specific resources within a habitat type (fourth order) [16]. The choice of the appropriate order for analysis depends on the specific research question being addressed but also on the resolution of the collected data.

Resource selection functions (RSFs) can be used to identify patterns in habitat preference [9,16,17]. Resource selection functions are statistical models used to estimate the probability of an animal selecting a particular type of resource, in our case habitat types, within a landscape. These models can be used to compare the availability of different habitat types in a specific area with the frequency of their use by the animal of interest [16,17]. If habitat selection would be random, animals would use different habitat types in proportion to their availability in the environment. However, when animals exhibit disproportional use of certain habitat types, it indicates a preference or avoidance of specific habitats. RSFs provide a valuable tool for investigating habitat selection patterns and allow researchers to understand factors influencing habitat selection and which resources may drive the selection towards a certain habitat [16].

To gain a comprehensive understanding of an animal's habitat use and requirements, it is therefore crucial to investigate habitat selection across various periods within an animal's life cycle. By considering both spatial and temporal aspects of habitat selection, researchers can unravel the complexity of resource use patterns and the factors driving resource selection decisions by animals.

Activity pattern outside the breeding period

Energy requirement can differ among different periods during the life cycle of an animal. During the breeding period, animals experience a high demand for energy as they need to meet their own metabolic needs and provide for their offspring. At the same time this period is characterized by increased food availability, which can help to offset the energetic requirements [18]. The non-breeding period however also presents unique challenges, especially in temperate regions. Harsh conditions prevail during this time, with dropping temperatures limiting resource availability and simultaneously increasing the energy expenditure for thermoregulation [19–22].

Therefore, the energy derived from resources must be allocated to different activities during the annual life cycle [18,23]. Throughout the reproductive period, energy allocation is allocated to both survival and reproduction. However, the two fitness components are in a trade-off relationship with each other. High energy investment in reproductive effort for a given breeding attempt is expected to trade off with survival [23–25] or future reproductive success [26,27]. During the non-breeding period energy is mainly allocated to survival [28,29] or , if possible, stored in preparation for the upcoming breeding investment [4,30].

To navigate the energetic challenges of the different periods, animals should strive to maximize their energy intake while minimizing the energy expended during foraging activities [31]. However, the level of activity required for foraging is also influenced by the environmental conditions within the animal's home range. Favourable habitat conditions can enable animals to obtain food with less movement and time investment [32,33]. Both meteorological conditions and prey availability play significant roles in shaping foraging behaviour and can impact the energy expenditure associated with foraging activities.

Animal-borne loggers that measure the animal's acceleration in three orientations (heave, surge, sway) can be utilized to quantify individual movement. These measurements provide the basis for calculating the dynamic body acceleration (DBA), which has been found to be strongly correlated with energy expenditure [34,35]. Additionally, by analysing the patterns in accelerometer data, it is possible to identify different behaviours, contingent upon the resolution of the data and the kinematics of the behaviours [36]. The probability of accurately assigning a specific behaviour to a given acceleration data pattern decreases as the sampling resolution becomes lower and the kinematics of behaviours become faster [36]. While lower sampling resolution enables longer sampling periods, it may not capture the full range of behaviours with sufficient detail. Thus, there is a trade-off between sampling duration and behaviour classification accuracy that needs to be carefully considered based on the specific goals of the study [36]. Longer sampling periods with lower resolution may be appropriate for capturing general activity patterns or long-term trends, whereas higher resolution sampling is required for finer-scale behaviour analysis and accurate discrimination between different behaviours. Ultimately, researchers must weigh the desired level of behavioural detail against the available sampling time to determine the optimal balance for their study.

Combining information on movement and the according expected energy expenditure with knowledge on environmental conditions could reveal how these conditions affect activity patterns in animals during the colder season.

Annual survival and reproductive success

The survival and reproductive success of animals depends on various internal (individual quality) and external (environmental conditions) factors. Environmental conditions, including food availability and weather, can impact an animal's survival and reproduction [22,29,37–39]. Assessing the impact of environmental conditions on an animal's fitness poses challenges due to the fluctuations that occur over time and across different spatial locations. To thoroughly investigate the influence of environmental factors on an animal's survival and reproductive success throughout its life cycle, it becomes essential to have high-resolution data that captures both temporal and spatial variations. Furthermore, individuals within a species may not all respond in the same way to the same environmental conditions [40–43]. Intrinsic differences among individuals, often correlated with individual quality, play a role in how they are affected when faced with challenges. However, quantifying such intrinsic quality differences is difficult, and researchers often rely on proxies that reflect or correlate with individual quality. In birds, traits like melanin-based coloration [44–46] or glucocorticoid responses to environmental pressures [47–50] are correlated with fitness and are therefore employed as indicators of the quality of an individual.

Studying how various extrinsic and intrinsic factors impact animal survival and reproduction is not only challenging because of the difficulty to assess the different factors, but also because of their different pathways of action [18,51]. Many factors are thought to affect survival of animals directly and indirectly at the same time. For instance, environmental conditions might reduce an animal's access to food and therefore directly affect its survival, but it may also increase reproductive costs which again act on survival, creating an indirect link between environmental conditions and survival. Furthermore, peak investment in reproduction can be dependent on the sex and the stage of reproduction, reproductive costs may therefore act differently on the sexes depending on their role within reproduction [40,52,53]. Therefore, it is important to consider the different pathways among which environmental and individual factors are able to affect animal fitness over time and if these fitness consequences are sex specific. Such analyses require careful design, rigorous data collection, and advanced statistical methods to disentangle the direct and indirect effects of various factors on animal survival and reproduction.

Using hierarchical models incorporating live-dead encounter and fecundity data allows to estimate the direct and indirect effects of intrinsic and extrinsic covariates on survival and reproductive performance [54].

Study species

The Western barn owl (*Tyto alba*) is a nocturnal bird of prey inhabiting agriculturally dominated landscapes. In central Europe, the breeding period extends from February till September [55] and is followed by a resident wintering period [56,57]. Harsh winters with prolonged snow cover affects the species demography by increasing adult as well as juvenile survival [29]. With a combination of increased energy demand due to low temperatures and decreased prey accessibility due to increased snow covers, harsh winter can act as a bottleneck for whole populations [29].

The main prey of barn owls in central Europe are small mammals, mainly *Arvicola*, *Microtus* and *Apodemus* species [58]. Small mammal populations across Europe underly a certain fluctuation among but also within years [59–62]. Within year fluctuations can be highly dependent of the habitat the small mammals are inhabiting. Agriculturally dominated areas underly strong seasonal structural changes with vegetation growth in spring and summer followed by a sudden change during harvest. Harvest can affect small mammal availability for predators either directly through decrease of small mammal population size, or movement of the potential prey towards less disturbed habitats [63–

67]. The resulting seasonal change in spatial distribution and population size of prey is likely able to influence behaviour and fitness of their predators.

The study population of barn owls is located in western Switzerland and is almost exclusively breeding in the more than 400 nest boxes which have been installed throughout the region since 1985. Within the frame of the long-term standard monitoring all breeding adults are captured and breeding success is monitored.

Aim and outline of the thesis

In this thesis, I investigated ecological questions of year-around habitat selection, movement related energy expenditure outside the breeding season, and animal fitness within the annual-cycle, contributing to a better understanding of the non-breeding period of barn owls and other birds of prey in general. To do this, I integrated data from long-term population monitoring, extended movement tracking, and year-round monitoring of prey availability. First, I developed new insights into patterns of habitat selection outside the breeding season, revealing seasonal differences in barn owl habitat choice. Next, I investigated the influence of weather conditions, habitat composition and prey availability on activity during the non-breeding period, providing new insights into activity patterns during an energetically demanding period. Finally, I investigated the direct and indirect impacts of environmental factors and individual traits on barn owl fitness, highlighting sex- and period-specific fitness consequences.

While it has been shown that barn owls experience increased mortality in winter, less is known about actual habitat selection and underlying prey distribution in agricultural landscapes. In the first chapter of my research, I therefore explored the habitat preferences of barn owls in relation to agricultural land use and prey availability during the non-breeding season. In a first step, I quantified the size and spatial distribution of breeding and non-breeding home ranges of barn owls and determined the specific habitat types preferred by barn owls during the non-breeding period. In a second step, I assessed whether this preference is influenced by the availability of prey during the non-breeding period. In particular, I investigated whether the availability of prey differed between habitats during the breeding and non-breeding seasons to determine the role of changing prey availability in shaping barn owl habitat selection.

Expanding on the findings of my first chapter, my aim in the second chapter was to investigate the energetic implications of meteorological conditions, prey availability on barn owl activity. Given the demanding and energy-intensive nature of the non-breeding period, my main focus was to investigate the factors that contribute to barn owls' ability to navigate through this period by optimising energy efficiency. As a first step, I examined activity on a broader scale by looking at nocturnal and seasonal activity patterns. In my previous chapter, I indicted that barn owls shift their habitat selection towards prey rich habitat types with nearby biodiversity structures. In order to better understand the selective pressure behind these findings, I investigated whether owls inhabiting areas with high prey abundance and/or perching opportunities show differences in activity patterns. As activity is strongly correlated with energy expenditure, I am able to discuss the possible energetic consequences of meteorological conditions and prey availability on energetic investment during winter. I furthermore investigated whether owls responded differently to prey availability depending on sex and plumage coloration.

In my third chapter I investigated how prey availability and intrinsic factors (such as individual quality and experience) are related to annual reproductive success and survival. A comprehensive understanding of the dynamics of barn owl fitness in relation to individual quality and food availability is critical to increase our understanding of their ecology. The study aims to explore the correlation between prey availability, intrinsic factors, and breeding success, as well as annual survival. Given the considerable variation in prey availability throughout the year, a crucial objective is to determine the specific timing during the annual cycle when prey availability significantly impacts breeding success and survival. Another important aspect of the investigation is to assess whether breeding success incurs reproductive costs on survival and if these costs are comparable between males and females. Given the different roles of sexes during reproduction, I paid particular attention to the sex-specific costs of reproduction on survival. To explore the above-mentioned aspects I integrated capture, mark re-capture and dead recovery data, individual measurements, brood surveys, and prey availability into a hierarchical path analysis.

Chapter 1:

Prey availability and its influence on habitat selection during the non-breeding period in a sedentary bird of prey

Chapter 1

Prey availability and its influence on habitat selection during the non-breeding period in a sedentary bird of prey

Roman Bühler[1,2], Kim Schalcher[2], Robin Séchaud[2,3], Stephanie Michler[1], Nadine Apolloni[1], Alexandre Roulin[2] and Bettina Almasi[1]

[1]Swiss Ornithological Institute, Seerose 1, CH-6204, Sempach, Switzerland.

[2]Department of Ecology and Evolution, University of Lausanne, Building Biophore, CH-1015, Lausanne, Switzerland.

[3]Agroecology and Environment, Agroscope, Reckenholzstrasse 191, CH-8046, Zurich, Switzerland

Chapter Status:

Published in Movement Ecology

https://doi.org/10.1186/s40462-023-00376-3

Authors contributions:

All authors designed the project, A. R. and B. A. funded the research. R. B., R. S. and K. S. collected data. R. B. and B. A. analysed data. R. B. wrote the manuscript, with significant contributions of all co-authors. The authors read and approved the final manuscript.

Bühler *et al. Movement Ecology* (2023) 11:14
https://doi.org/10.1186/s40462-023-00376-3

Movement Ecology

RESEARCH

Open Access

Influence of prey availability on habitat selection during the non-breeding period in a resident bird of prey

Roman Bühler[1,2*], Kim Schalcher[2], Robin Séchaud[2,3], Stephanie Michler[1], Nadine Apolloni[1], Alexandre Roulin[2] and Bettina Almasi[1]

Abstract

Background For resident birds of prey in the temperate zone, the cold non-breeding period can have strong impacts on survival and reproduction with implications for population dynamics. Therefore, the non-breeding period should receive the same attention as other parts of the annual life cycle. Birds of prey in intensively managed agricultural areas are repeatedly confronted with unpredictable, rapid changes in their habitat due to agricultural practices such as mowing, harvesting, and ploughing. Such a dynamic landscape likely affects prey distribution and availability and may even result in changes in habitat selection of the predator throughout the annual cycle.

Methods In the present study, we (1) quantified barn owl prey availability in different habitats across the annual cycle, (2) quantified the size and location of barn owl breeding and non-breeding home ranges using GPS-data, (3) assessed habitat selection in relation to prey availability during the non-breeding period, and (4) discussed differences in habitat selection during the non-breeding period to habitat selection during the breeding period.

Results The patchier prey distribution during the non-breeding period compared to the breeding period led to habitat selection towards grassland during the non-breeding period. The size of barn owl home ranges during breeding and non-breeding were similar, but there was a small shift in home range location which was more pronounced in females than males. The changes in prey availability led to a mainly grassland-oriented habitat selection during the non-breeding period. Further, our results showed the importance of biodiversity promotion areas and undisturbed field margins within the intensively managed agricultural landscape.

Conclusions We showed that different prey availability in habitat categories can lead to changes in habitat preference between the breeding and the non-breeding period. Given these results we show how important it is to maintain and enhance structural diversity in intensive agricultural landscapes, to effectively protect birds of prey specialised on small mammals.

Keywords Full annual cycle, Non-breeding period, GPS, Small mammals, Resource selection, *Tyto alba*, Bird of prey, Habitat selection, Biodiversity promotion areas

---

*Correspondence:
Roman Bühler
roman.buehler@vogelwarte.ch
Full list of author information is available at the end of the article

Introduction

Annual cycles organize living beings in different periods (e.g., dispersal, migration, breeding, non-breeding) which can vary in duration and geographical location depending on the species [1]. In temperate regions, periods are generally accompanied by meteorological changes, where lower temperatures in autumn and winter lead to changes in productivity on several trophic levels, affecting primary producers and their consumers [2]. Species respond to changes in resource availability with different strategies. While migratory species leave breeding habitats when resources decline and move to areas with higher resource availability, resident animals react to changes in resources by shifting their hunting grounds and/or exploiting alternative resources [3, 4]. Such seasonal changes do not only affect individual performance in their current state but can also carry over and affect future events, such as reproduction [5]. Considering the important influences of the non-breeding period on individual performance and survival and the resulting effects on population development, this demanding period should receive more attention, especially in the light of species conservation.

Birds react sensitively to food shortage, making food availability one of the most important factors to address in conservation research [6–10]. Local changes in food availability potentially have a high impact on sedentary animals with high prey specialisation, as they are limited in flexibility regarding resource exploitation. For birds of prey specialised on small mammals, resource availability fluctuates as prey densities may show multi annual cycles, as well as density changes within an annual cycle [7, 11–13].

Within the annual cycle, fluctuations in prey densities in a habitat can be highly dependent on habitat characteristics. Small mammals living in semi-natural habitats, such as agricultural dominated landscapes, are often exposed to sudden periodic disruptions. These disruptions affect local population densities within a short period of time and have the potential to influence future densities on a large scale [14, 15]. An example of such a disruption is the harvesting of intensively managed crop plantations: while small mammal abundance within seasonal crop may be high in summer, harvesting leads to sudden population changes within these areas [14–18]. The main drivers of such population changes after harvest are either direct mortality due to mechanical treatment, increased predation due to reduced vegetation cover, or a shift of activity in less disturbed and more suitable habitats [14, 18–20]. Biodiversity promotion areas (e.g., wildflower strips, rotational fallows), semi natural habitats (hedges) and field margins as well as perennial crops represent such less disturbed habitats [18, 21–26]. These habitats can act as refuge during periods of disturbance and can allow small mammals to reuse or recolonise intensively managed agricultural fields after disturbance [23–25, 27]. The resulting seasonal change in spatial distribution of prey is likely able to influence habitat selection of their predators. Thus, we hypothesize that the preference for different habitat categories should be plastic and shift according to the availability of resources within those habitats at the corresponding time.

As a resident bird of prey, the barn owl (*Tyto alba*) is sensitive to reduced food availability [28] and harsh winter conditions [29]. At low ambient temperatures, the metabolic rate increases, resulting in higher energy requirements to cover baseline energetic demand [30, 31]. At the same time prey availability can be drastically reduced due to low abundance and activity of small mammals [7, 11, 12]. Additionally, harsh winters with a closed snow cover reduce accessibility of prey [29]. If such unfavourable circumstances persist for several days (starvation limit ~ 7 days, [31]) this not only affects the survival of individuals but can also lead to the extinction of regional populations [29].

With agricultural intensification the European barn owl suffered from a strong decline across Europe and is listed as vulnerable in Switzerland [32]. The availability of nesting sites and foraging habitats are the most important factors affecting population size [33, 34]. The installation of nest boxes can increase breeding success, but probably only has little effect on the survival outside the breeding period. The habitat requirements of barn owls, especially during the non-breeding period, are still not well studied. We need a better understanding of the habitats in which prey occur at sufficiently high densities during the non-breeding period and are also accessible to predators. Identifying these habitats is key to implementing further conservation measures to ensure the continued existence of resident birds of prey in a fast-changing landscape. In this study, we (1) quantified barn owl prey availability in different habitats throughout the annual cycle, (2) quantified the size and location of barn owl breeding and non-breeding home ranges, (3) assessed habitat selection in relation to prey availability during the non-breeding period, and (4) discussed the changes in habitat selection between the breeding and non-breeding period. We expect to see a seasonal shift in prey availability from intensively managed to less disturbed habitats and a corresponding shift in predator habitat selection towards these prey rich habitats.

Material and methods

Study area and study species

The study was carried out in western Switzerland (46°49′ N, 06°56′ E) in an area of ~ 1000 km^2. The study area consists of four geographical regions (see Additional file 1: S1.1), two lowland regions dominated by intensive arable farming (plain of Orbe, plain of the Broye), and two hilly regions dominated by grazing and arable farming (Haut-Fribourg, Gros de Vaud). One inhabitant of such agriculturally dominated landscapes is the barn owl (*Tyto alba*), a medium-sized raptor which mainly preys on small mammals. The Swiss population almost exclusively breeds in nest boxes installed in or on buildings. More than 400 nest boxes for barn owls have been installed throughout the region since 1985. The breeding period extends from February to September [35], followed by a resident non-breeding period.

Small mammal monitoring

While *Arvicola, Microtus, and Apodemus* species represent the staple prey of European barn owls in Central Europe, barn owls are also known to prey on other small mammals like *Myodes* and *Sorex/Crocidura* species [34, 36]. Voles (*Arvicola* sp., *Microtus* sp.*)* inhabit open habitats, especially grasslands, and are partly active below ground using rather small areas (e.g., common vole, *Microtus arvalis*: 200 m^2) [15, 27, 37]. *Apodemus* species live in open habitats as well as wooded areas, are mainly active above ground, and can show large home ranges (e.g., wood mice, *Apodemus sylvaticus*: 4900–14,400 m^2) [18]. We monitored potential prey for barn owls within our study region from 2015 to 2021 by using two indirect methods: First, we counted signs of recent vole activity (heaps, holes, and runways) along short transects (5×1 m [38]). Such signs are unique and well distinguishable from naturally occurring variation in vegetation [39]. To ensure that the signs were from recent activity, we looked for fresh droppings and remains of recently cut vegetation. Counting such signs of activity gives us information about the presence and activity density (combination of activity and abundance) of voles. Second, to assess the availability of all small mammal species, we laid plates covered with a thin layer of graphite along the transects (method adapted from [40]). As small mammals walk across these track-plates they leave distinct traces on the thin graphite layer. The number of these traces provides information about presence and the activity density of small mammals. Combining both methods, information for the presence and activity density of both voles and total small mammals are obtained.

In each of the four geographical regions in our study area, we defined four plots of 9 km^2 (see Additional file 1: S1.1) where small mammal activity density was surveyed in five different habitat categories (crop rotation, grasslands, border structures, forest, biodiversity structures) every second month (six sessions per year). Nine transects were walked in each habitat category per plot and, region and recent signs of vole signs (heaps, hole, runways) were counted. In addition, one track-plate covered with graphite was laid out along each transect during three consecutive nights. Small mammal traces were subsequently counted on each track-plate. This resulted in a total of 720 transects and an equal number of track-plates for each 2-months session (see Additional file 1: S1.2).

Track-plates and transect counts correlate well with estimates of relative abundance from live trapping [40, 41], are less time-consuming than live traps, and are therefore best suited to be used for large-scale small mammal monitoring. Track-plate and transect counts reflect the activity density of potential prey and are likely to correlate with prey availability, as areas with more active [42] and abundant prey are generally preferred by predators. As vole populations in central Europe vary synchronously over large spatial scales [43], we are confident that the spatial resolution of our small mammal monitoring design is appropriate to estimate prey activity density over the scale of our geographical regions.

GPS deployment and home range

To study habitat use during the non-breeding period, we equipped adult barn owls with GPS devices. We captured the owls during the breeding period when they were feeding the nestlings, by placing a sliding door at the nest box entrance, which the owl triggers when it enters [44]. After capturing, the individual was measured, and its sex determined based on the presence or absence of a brood patch. The GPS-tag (Gipsy-5 and Axy-Trek, Technosmart, Italy) was combined with a VHF-transmitter (µTag, Swiss Ornithological Institute) and attached as a wing loop harness with spectra tubular tape (4.7 mm, polyethylene, Bally Ribbon Mills, US). The combined tag weighted < 13 g (which is < 5% of body mass, mean body mass of birds before tagging: 297 g, range: 260–440 g, limit for equipment: > 260 g). We used two different GPS modules (Gipsy-5 and Axy-Trek) which both must be retrieved to read the data. GPS tags were programmed to start with a delay to capture locations as far into non-breeding period (October to February) as possible. Once activated, one position was recorded every hour for two halfnights a week (7–12 p.m. and 0–4 a.m. UTC), resulting in an average of 6.6 locations per week. The VHF tag was programmed to be active for 1 week the following spring. During this week, we searched for the tagged individuals, checked the status of the birds and recovered the GPS tags of dead owls. Individuals breeding in the year after GPS deployment were recaptured during chick feeding as described above. Ten days before GPS deployment for the non-breeding period, the owls were captured a first time to be equipped with a GPS tag to record breeding habitat use for another study [44, 45]. For this study purpose GPS tags were programmed to recorded with a resolution of 1 location every 60 s for the following 10 days. After these 10 days, the owls were re-captured and equipped with the GPS for the non-breeding period. The breeding period data are used in this study to compare size of breeding and non-breeding home ranges, their overlap and distances from the breeding nest box to the centroid of the breeding and non-breeding home ranges. All GPS data have been uploaded to Movebank (non-breeding period ID: 1433219445; recovery rate of GPS tags in 2018: 55%, females: 22 out of 37, males: 20 out of 39; 2019: 68%, females: 22 out of 41, males: 37 out of 46, and breeding period ID: 231741797).

Throughout the non-breeding period (September–February), we obtained 10,142 GPS locations from 65 different individuals (males: 32, females: 33) from 74 (out of 101) deployments (duration of recording: 31–180 days, mean: 132 days). GPS data were filtered for duplicated locations and aberrant positions (528 points removed). The latest GPS modules (Axy) included triaxial accelerometers, resulting in slightly higher energy consumption compared to the GPS-only modules (Gipsy). To compensate for this difference, the Axy modules were programmed to skip fixing locations during periods of bird inactivity. To obtain comparable data, we resampled the Gipsy data by removing locations which were close in time and space, i.e., where the bird appeared to be inactive (birds that did not move more than 30 m within 120 min). The resampling process removed 1195 locations, and we ended up with a dataset of 8419 locations.

Non-breeding and breeding home range sizes were calculated using a minimum convex polygon (MCP), containing 95% of locations for each animal. We used the function hrBootstrap [46] to assess the saturation of our estimated home ranges. We considered home ranges to be saturated if the increase in area between the last 3 iterations of the stepwise increase did not exceed 15%. We were able to estimate stable non-breeding home ranges for 51 (males: 27, females: 24) out of 74 deployments. Home ranges were estimated from 30 up to 212 locations per individual with a mean of 130 locations (females: mean: 141, range: 38–194, males: mean: 119, range: 30–212). For 46 (males: 24, females: 22) of the 51 non-breeding home ranges, data were available to calculate breeding home range of the previous reproductive period. Breeding home range was estimated based on 370 up to 5001 locations per individual with a mean of 3086 locations (females: mean: 3185, range: 1017–4516, males: mean: 2995, range: 370–5001).

Habitat variables and home range composition

Information on the coverage of forest, urban area, hedges, single trees, roads (field path, minor, and major roads, highways, railways) and border structures (1 m buffer around roads) was obtained from the TLM3D database of the Swiss topographic institute (TLM3D, resolution: 0.2–3 m, Federal office of topography: Swisstopo, Seftigenstrasse 264, 3084 Wabern). The different categories were buffered to create the layers used in the final analysis (for details see Additional file 1: S1.3). Agricultural land was divided into four different habitat categories: intensive grassland (intensively managed pastures and meadows), extensive grassland (extensively managed pastures and meadows), crop rotation, wildflower strips and rotational fallows. Information on these habitat categories were extracted from the cantonal GIS-layer (canton Vaud: all agricultural fields, canton Fribourg: only permanent cultures) and supplemented with data from habitat mapping in the canton Fribourg (for details see Additional file 1: S1.4/1.5). Finally, hedges, single trees (source: TLM3D) as well as wildflower strips and rotational fallows (source: cantonal layers, part of biodiversity promoting areas) were summarized under the term biodiversity structures. To obtain habitat composition at the home range level during non-breeding period, coverage of the five main habitat categories (crop rotation, extensive grassland, intensive grassland, forest, and urban area) within each of the 51 previously calculated non-breeding MCP was extracted.

To model resource selection within non-breeding home ranges (third order selection [47]), we randomly selected available locations at a ratio of 1 used versus 100 available locations within each home range (95% MCP). With the 95% MCP boundaries used for sampling of available locations, only used locations within the 95% MCP were considered for the analysis (7534 locations used and 753,400 available locations). We then placed a 75 × 75 m square over each used and available location, hereafter referred to as focal area. This focal area was divided into a central 25 × 25 m (containing the GPS point) and eight surrounding 25 × 25 m grid cells. From each grid cell the proportion of area covered by the 5 habitat categories (crop rotation, intensive grassland, extensive grassland, urban area, forest) was extracted and the central grid cell (of the 3 × 3 cell grid) was weighted twice as much than the surrounding grid cells (0.2 vs 0.1). Additionally, the number of different habitat categories was extracted and used to describe structural richness. By considering a broader and weighted focal area rather than just the central grid cell, we minimized the risk of missing meaningful signals due to GPS localization errors (mean accuracy with settings used: 20 m). Focal areas for which less than 50% and more than 120% of their total area was described, were excluded from the analysis. This was the case whenever information describing the area was missing, or the same area was described by contradictory, overlaying layers

(605 removed out of 7534 used and 85,303 removed out of 753,400 available locations). For an initial analysis of habitat selection within the home range, we reduced our dataset to one habitat category per focal area by assigning each used and available location the category with the highest coverage within the focal area (dominant habitat category). We removed all locations for which the dominant habitat category on the focal area was unknown (used: 42 removed out of 6929, available: 6968 removed out of 668,097).

Statistical analysis

Vole and small mammal activity density

The numbers of vole signs (transect method, hereafter vole activity density) and the number of small mammal traces (track-plate method, hereafter small-mammal activity density) were analysed separately by fitting a generalized additive model (GAMM, [48]). While the total number of traces or signs, on the track-plates or along transects, served as response variable, region, observation round, habitat category, and temperature (for transects: mean from 10 days before transect counts, for track-plates: mean of the 3 days on which track-plates were exposed) were included as explanatory variables. Fitted values for a given time for each habitat structure in each region are estimated separately for transect and track-plate counts and are used as an index of vole and small mammal activity density (abundance, and activity). Model fit was evaluated using shinystan [49], which provides visual and numerical summaries of model parameters and convergence diagnostics for Markov Chain Monte Carlo (MCMC) simulations.

To illustrate potential differences between the breeding and the non-breeding period in vole and small mammal activity densities, we visualized the vole and small mammal activity density for the November–December sampling round (non-breeding period) and the May–June sampling round (breeding period) in the "Plain of Orbe" region in 2018. To do so, we multiplied the activity density by the area covered by each habitat category within a 25 m resolution grid (Fig. 1). Using the same procedure, we interpolated small mammal and vole activity density for our 75 m × 75 m focal areas in the analysis later on.

Because the two activity densities showed different patterns depending on habitat types and period, with different implications for barn owl availability and accessibility, they were interpreted and analysed separately in the following steps.

Home range size and location of home ranges

To assess if home range size differed between male and females and between periods, we ran linear models with log-transformed home range size as the response variable and period (breeding/non-breeding), sex and year as explanatory variables. Individual identity was included as random effect. To assess if the spatial distributions of locations of breeding and non-breeding home ranges differ, we measured (1) the distance from the centroid of the breeding home range to the breeding nest box, (2) the distance from the centroid of the non-breeding home range to the previous breeding nest box, (3) the distance from the centroid of the non-breeding home range to the future breeding nest box. We then built a linear model with log-transformed distance as response and the type of distance (1,2,3) as well as sex as explanatory variable. Individual and nest box ID were included as random effects. Posterior distribution was obtained by simulating 1000 values from the joint posterior distribution of model parameters using the "simulate_model" function of the "parameters" package [50]. The means of the simulated posterior distribution were used as estimates and the corresponding 2.5% and 97.5% quantiles as the upper and lower bounds of the 95% credible interval (CrI). Effects were interpreted as meaningful when they differed from 0 (95% CrI not containing 0).

Resource selection

To compare habitat variables at used (GPS fixes) versus available locations within the owls' home range (third-order selection [47]), we used a resource selection function (RSF; [51]). The sampling design used to collect our data (1 fix/hour) should meet the assumption of independence. To generate a population level RSF function, we used a generalized linear mixed effects model with a weighted logistic regression, binomial error distribution and a logit-link function (glmmTMB; [52]).

To account for the non-independence of the data derived from the same individual we included a random intercept for each individual and deployment (hereafter tag deployment) in our models [53]. Following the recommendation of Muff and Fieberg [54] we included random slopes for our explanatory variables whenever possible to account for individual-specific variation in habitat selection.

First, we built an RSF with 6887 used and 661,129 available focal areas (ratio: 1:96), as response variable in relation to the dominant habitat category of the focal area (intensive grassland, extensive grassland, crop rotation, urban area, forest), biodiversity structure (presence or absence of hedges, trees, wildflower strips, rotational fallows within the focal area), structural richness (number of different habitat categories within the focal area), and sex (male/female). To determine whether the presence or absence of biodiversity structures influenced habitat category choice, we included the interaction with the dominant habitat category in a second model. We included a

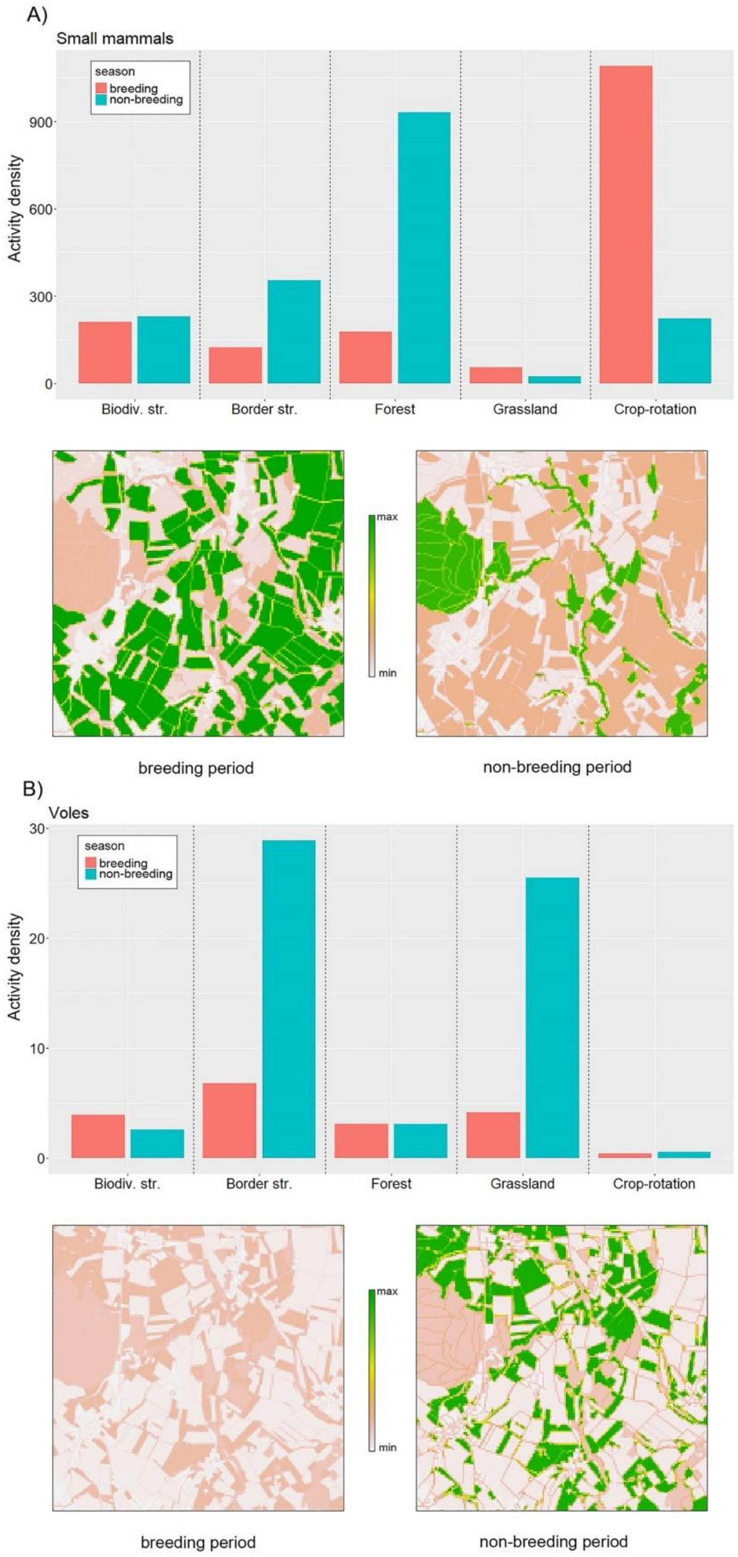


Fig. 1 **A** Small mammal and **B** vole activity densities during breeding (May–June, red) and non-breeding period (November–December, blue) for biodiversity structures, border structures, forest, grassland and crop-rotation fields within the region Orbe for the year 2018. Lower graphs: visual representation of small mammal and vole activity density on the landscape level for owl breeding and non-breeding period (left: breeding period, right: non-breeding period). Colour scale indicates the activity density value for a certain area and is comparable within indices but not between

random intercept for each individual and deployment (hereafter tag deployment) and random slopes for habitat category, biodiversity structure, and structural richness in the model. To meet the assumptions of an inhomogeneous point process model, we assigned a weight of 5000 to available locations and a weight of 1 to all used locations [55, 56]. In our sensitivity analysis, which we performed with ratios of 1:10, 1:50 and 1:100, estimates stabilized at a ratio of 1:10. For the final analysis, we chose the highest ratio of 1:100, because computation time was not limiting in our case. The exponential value from the β estimates is referred to as relative selection strength (RSS) [57]. RSS values from used-available studies do not represent true probabilities but are proportional to the probability of selection. We choose crop rotation as the reference level for habitat category because it is the most abundant habitat category within owl home ranges (Fig. 2).

In a second step, we wanted to test whether the activity density of small mammals or voles per focal area influences selection and whether the presence of biodiversity structures influences selection. To calculate vole or small mammal activity density per focal area, the area of the specific habitat category of the focal area (crop rotation, extensive grassland, intensive grassland, border structures, biodiversity structures) was multiplied by the corresponding vole or small mammal activity density (region and time) and summed up over the focal area. This gives us one value for vole and one for small mammal activity density per focal area. We then ran a second glmmTMB model with vole and small mammal activity density per focal area, the presence or absence of biodiversity structure and sex as explanatory variables. Tag deployment (unique identifier for each individual per year) was included as random intercept and vole activity density per focal area, small mammal activity density per focal area, and biodiversity structures were included as random slopes.

In a third step, we modelled whether focal area selection is dependent on the combined prey activity density within the different habitat categories (total prey activity density). To combine the activity density of voles and small mammals per habitat category and focal area, we first multiplied the area of each habitat category (crop rotation, grassland, border structures, biodiversity structures) within each focal area by the corresponding value for the activity density per habitat category and focal area for voles and small mammals separately. These activity densities per habitat category and focal area, after being centred and scaled, were summed to obtain a total activity density per habitat category and focal area. We then ran a model with total prey activity density per foraging habitat category and focal area, sex and structural richness as explanatory variables. Tag deployment was included as random intercept and prey activity density for each habitat and focal area as random slopes. To reduce model complexity and allow the model to converge the two types of grassland (extensive and intensive) were merged.

As the focus of the analyses of the second and third step described above was on prey availability in the

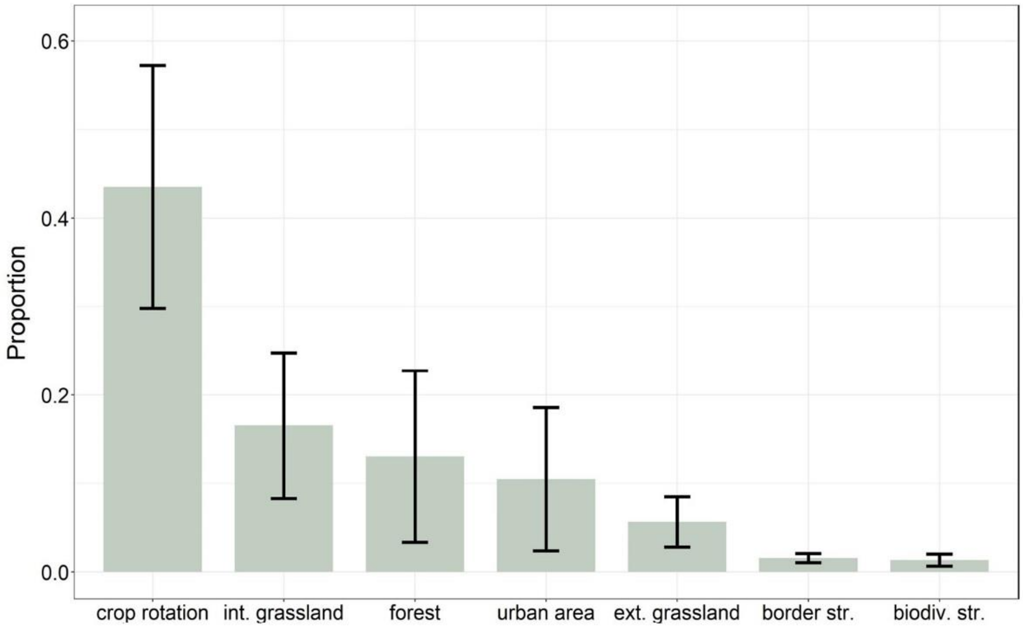


Fig. 2 Visualisation of the proportion of habitat categories present within the 51 non-breeding home ranges, with the corresponding standard deviation

foraging habitats of barn owls, we excluded all focal areas where the potential foraging habitat was less than 20% (< 1125 m^2) of the focal area. Therefore, focal areas with forest cover or urban covering more than 80% of the focal area were classified as unsuitable foraging areas [44, 58] and excluded from this part of the analyses. This procedure removed a total of 947 used locations and 123,551 available locations, resulting in a dataset of 5982 used versus 544,546 available locations (ratio: 1:91).

All numeric variables were scaled before being entered into the models. To obtain the posterior distribution, we directly simulated 1000 values from the joint posterior distribution of the model parameters using the "simulate_model" function of the package "parameters" [50]. The means of the simulated posterior distribution were used as estimates and the according 2.5% and 97.5% quantiles as upper and lower limits of the 95% credible interval (CrI). Effects were interpreted as meaningful when they differed from 0 (95% CrI not containing 0). To validate our models, we followed the method outlined by Johnson et al. [59] by regressing observed against predicted data (cross validation) (for details see Additional file 1: S2.1). All analyses were performed using the software R 4.1.0 [60].

Results

Vole- and small mammal indices

Both the vole and small mammal activity density showed fluctuations among sampling periods, regions, and years (see Additional file 1: S2.2 and S2.3 for detailed information). Small mammal activity density showed a similar pattern in crop-rotation and grasslands, with high values during the breeding period followed by a decline in autumn. Small mammal activity densities in forest and biodiversity structures also followed cyclic fluctuations but tended to reach their maximum later in the year, reaching into the non-breeding period. At the landscape level, this resulted in condensed small mammal availability during the non-breeding period, with high activity densities in and along forests and border structures and lower activity densities in adjacent agricultural areas (Fig. 1). For vole activity densities, grassland and border structures showed a pronounced difference between breeding and non-breeding periods: while both habitat categories showed low activity densities during the breeding period, they showed relatively high values during the non-breeding period (Fig. 1), resulting in a patchy distribution of vole availability at the landscape level during the non-breeding period compared to the breeding period.

Home range size, location, and composition

Non-breeding home range size at the 95% isopleth of the minimum convex polygon ranged from 1.1 to 46.8 km^2 (median: 6.8 ± 4.2 (MAD) km^2, n = 51). Males had a median non-breeding home range of 4.6 ± 4.2 km^2 (range: 1.1–46.8 km^2, n = 27) and females of 8.3 ± 3.3 km^2 (range: 4.0–25.3 km^2, n = 24). Breeding home range size ranged from 1.1 to 38.2 km^2 (median: 6.5 ± 4.9 km^2, n = 46). Males had a median breeding home range of 5.7 ± 4.2 km^2 (range: 1.1–12.8 km^2, n = 24) and females of 9.3 ± 6.4 km^2 (range: 2.4–38.2 km^2, n = 22). The mean home range size did not differ between the breeding and the non-breeding period (0.10, CrI: − 0.13 to 0.38, n = 97), but males generally had smaller mean home ranges than females (− 0.49, CrI: − 0.87 to − 0.14). Within sex we could not detect any difference in home range size between breeding and non-breeding period (0.01, CrI: − 0.54 to 0.52). (Details see Additional file 1: S2.4).

Median distance from centroids of non-breeding home ranges to the previous breeding nest box was 1.1 ± 1.0 km (range: 0.1–18.1 km, n = 51). There was a difference in the distance from centroids of non-breeding home ranges to the previous breeding nest box where males had shorter distances than females (median males: 0.9 ± 0.6 km, range: 0.1–5.3 km, n = 27, median females; 1.6 ± 1.7 km, range: 0.2–18.1 km, n = 24; − 0.62, CrI: − 1.20 to − 0.07). Median distance from centroids of non-breeding home ranges to the future breeding nest box was 1.0 ± 1.0 km (range: 0.1–21.8 km, n = 42), with no difference between males and females (median males: 1.0 ± 0.8 km, range: 0.1–4.0 km, n = 23, median females 1.2 ± 1.0 km, range: 0.3–21.8 km, n = 19; − 0.63, CrI: − 1.27 to 0.00). In 83% (19 out of 23) of the cases, the males bred in the same nest box as the previous year and females in 37% (7 out of 19) of the cases. (Details see Additional file 1: S2.5).

During breeding the median distance from the nest box to the centroid of the home range was 0.5 ± 0.4 km (range: 0.1–3.9 km, n = 46). There were no sex differences in the distance between the breeding home range centroid and the breeding nest box (median males 0.5 ± 0.3 km, range: 0.2–2.0 km, n = 24, median female 0.6 ± 0.5 km, range: 0.1–3.9 km, n = 22; 0.00, CrI: − 0.53 to 0.60). (Details see Additional file 1: S2.5).

The median overlap of non-breeding and breeding home range was 38 ± 20% (range: 0–69%, n = 46). The median overlap of male home ranges was 41 ± 16% (range: 7–69% n = 24) and 33 ± 20% (range: 0–61%, n = 22) for females.

Non-breeding home ranges contained predominately crop rotation fields (43.5 ± 13.4%) followed by grasslands (16.1 ± 8.4%, intensive grassland, 5.6 ± 2.8% extensive grassland). Forest (13.4 ± 10%) and urban area (10.7 ± 8.3%) also covered a substantial amount of area, whereas border structures (1.6 ± 0.5%) and biodiversity structures (1.3 ± 0.7%) only covered a small amount of area (Fig. 2).

Habitat selection

The resource selection function revealed that relative selection strength during the non-breeding period (RSS) (Table 1, Fig. 3) was highest for urban areas (RSS: 1.35 CrI: 1.09 to 1.63) followed by intensive grassland (RSS: 1.28 CrI: 1.07 to 1.55), extensive grassland (RSS: 1.07 CrI: 0.83 to 1.34) and was lowest for forest-dominated areas (RSS: 0.55 CrI: 0.41 to 0.72). RSS tells us the preference of the birds to choose any of the other categories over the reference category (crop rotation), given they are equally available and accessible. This means that the birds were 1.28 times more likely to choose areas dominated by intensive grassland than crop rotation if they were equally available. Further, the probability that a bird chose a location dominated by forest over one dominated by crop-rotation was 0.55 times lower. This gives the following, decreasing order of selection: urban area > intensive grassland > extensive grassland > crop rotation > forest. Both factors, structural diversity and the presence of biodiversity structures showed a positive estimate, but the effects were considered weak.

The presence of biodiversity structures had a positive effect on most habitat categories, but only the interaction with extensive grassland showed a meaningful effect (RSS: 1.42, CrI: 1.10 to 1.77) (Table 1, Fig. 3).

Habitat selection, biodiversity structures, and prey

To investigate the effect of biodiversity structures on the grassland preference found above, we calculated the vole and small mammal activity density per focal area and modelled the preference of owls as a function of vole and small mammal activity density within the focal area with biodiversity structures present or absent (Table 2, Fig. 4). The model estimates of the interaction of biodiversity structures and vole activity density per focal area suggested a positive selection when biodiversity structures were present (RSS: 1.23, CrI: 1.16 to 1.32, Fig. 4 A). The estimates of the interaction of biodiversity structures and small mammal activity density within focal area showed a weak negative effect if biodiversity structures were present (RSS: 0.68, CrI: 0.63 to 0.72, Fig. 4B). Generally, selection increased with increasing vole activity density in

Table 1 Resource selection function for used and available focal areas within the non-breeding home ranges of barn owls

Fixed effects	**Main effects β mean (95%CrI)**	**With interactions β mean (95%CrI)**
Intercept	− 13.20 (− 13.31 to − 13.09)	− 13.18 (− 13.30 to − 13.07)
Sex m	**− 0.13 (− 0.22 to − 0.07)**	**− 0.13 (− 0.20 to − 0.06)**
Habitat category		
Intensive grassland	**0.25 (0.07 to 0.44)**	**0.21 (0.03 to 0.39)**
Extensive grassland	0.07 (− 0.18 to 0.29)	− 0.13 (− 0.40 to 0.17)
Forest	**− 0.60 (− 0.90 to − 0.33)**	**− 0.64 (− 0.92 to − 0.34)**
Urban area	**0.29 (0.08 to 0.48)**	**0.29 (0.05 to 0.60**)
Biodiversity structures (present)	0.08 (− 0.10 to 0.28)	− 0.003 (− 0.19 to 0.20)
Structural richness	0.03 (− 0.05 to 0.11)	− 0.03 (− 0.20 to 0.11)
Intensive grassland × Biodiv. structures		0.13 (− 0.01 to 0.28)
Extensive grassland × Biodiv. structures		**0.35 (0.10 to 0.57)**
Forest × Biodiv. structures		0.16 (− 0.11 to 0.43)
Urban area × Biodiv. structures		0.07 (− 0.15 to 0.28)
Random effects	**Variance (± sd)**	**Variance (± sd)**
Deployment (intercept)	0.19 (± 0.44)	0.18 (± 0.43)
Intensive grassland (slope)	0.49 (± 0.70)	0.49 (± 0.70)
Extensive grassland (slope)	0.62 (± 0.79)	0.64 (± 0.80)
Forest (slope)	1.12 (± 1.06)	1.11 (± 1.05)
Urban area (slope)	0.61 (± 0.75)	0.63 (± 0.80)
Biodiv. structures 1 (slope)	0.57 (± 0.75)	0.56 (± 0.75)
Structural richness (slope)	0.10 (± 0.32)	0.10 (± 0.32)

We present the mean estimates of β and associated 95% credible interval of the posterior distribution of a logistic mixed effect model based on 65 individuals. Sex, habitat category, biodiversity structures and structural richness were introduced as explanatory variables, tag deployment as random intercept, and habitat category, biodiversity structures and structural richness as random slopes. The reference category is crop-rotation without biodiversity structures. First model without and second with interaction of habitat category with biodiversity structures

Effects whose credible interval does not include 0 are shown in bold

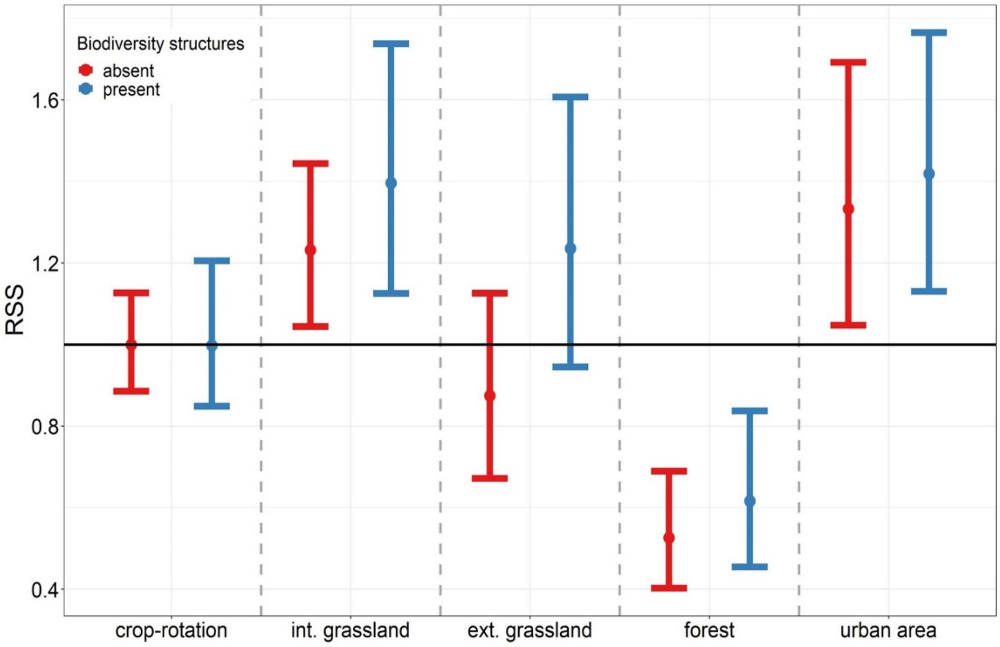


Fig. 3 Mean estimates of RSS (exp(β)) and associated 95% credible interval of the posterior distribution of a logistic mixed effect model based on 65 individuals. Estimates are presented for biodiversity structures absent (red) and present (blue) for each habitat category. Habitat category and biodiversity structures were included as random slope and tag deployment as random intercept the reference category for the relative selection strength is represented by crop-rotation without biodiversity structures. Values shown for females

Table 2 Resource selection function for used and available focal areas within the non-breeding home ranges of barn owls

Fixed effects	**β mean (95%CrI)**
Intercept	− 13.07 (− 13.17 to − 12.96)
Sex m	**− 0.20 (− 0.30 to − 0.08)**
Small mammal activity density/focal area	**0.15 (0.08 to 0.21)**
Vole activity density/focal area	**0.18 (0.08 to 0.29)**
Biodiversity structures (present)	0.13 (− 0.04 to 0.30)
Small mammal activity density/focal area × Biodiv. structures	**− 0.39 (− 0.47 to − 0.32)**
Vole activity density/focal area × Biodiv. structures	**0.21 (0.15 to 0.28)**
Random effects	**Variance (± SD)**
Deployment (Intercept)	0.13 (± 0.39)
Small mammal activity density/focal area (slope)	0.04 (± 0.20)
Vole activity density/focal area (slope)	0.14 (± 0.38)
Biodiversity structures (slope)	0.48 (± 0.69)

We present the mean estimates of β and associated 95% credible interval of the posterior distribution of a logistic mixed effect model based on 65 individuals. Sex, vole activity density per focal area, small mammal activity density per focal area, and biodiversity structures were introduced as explanatory variables, tag deployment as random intercept, and vole activity density per focal area, small mammal activity density per focal area and biodiversity structures as random slopes. Vole and small mammal activity density per focal area was modelled in interaction with biodiversity structures

Effects whose credible interval does not include 0 are shown in bold

the focal area. For small mammal activity density within focal area, selection increased only in the absence of biodiversity structures. In fact, selection decreased slightly for areas with increasing small mammal activity density if biodiversity structures were present, however the effect size was small.

Focal areas with increased activity density within intensive grassland (RSS: 1.22, CrI: 1.08 to 1.36), extensive grassland (RSS: 1.09, CrI: 1.01 to 1.20) and border structures (RSS: 1.15, CrI: 1.02 to 1.35) were selected (Table 3), while focal areas with increased activity density within

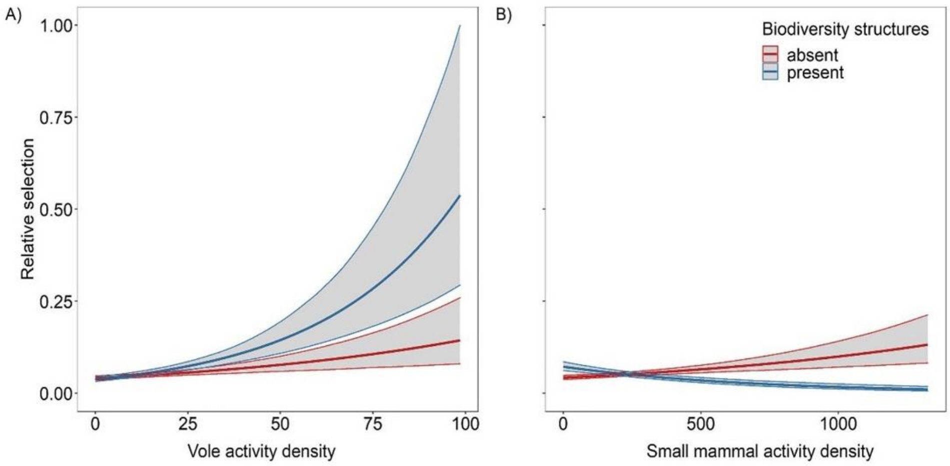


Fig. 4 Relative selection strength for focal areas in relation to vole activity density per focal area (**A**) and small mammal activity density per focal area (**B**) with (blue) and without (red) biodiversity structures. We present mean estimates of β and associated 95% credible interval of the posterior distribution of the logistic mixed effect model of Table 2. Analyses are based on 74 deployments of 65 individuals. Upper limit of the 95% CrI of the highest vole activity density per focal area with biodiversity structures present was set to 1

Table 3 Resource selection function for used and available focal areas within the non-breeding home ranges of barn owls

Fixed effects	**β mean (95%CrI)**
Intercept	− 13.05 (− 13.20 to − 12.91)
Sex m	**− 0.33 (− 0.53 to − 0.11)**
Total prey activity density intensive grassland/focal area	**0.20 (0.08 to 0.31)**
Total prey activity density extensive grassland/focal area	**0.09 (0.01 to 0.18)**
Total prey activity density biodiv. structures/focal area	**− 0.24 (− 0.34 to − 0.13)**
Total prey activity density crop rotation/focal area	0.03 (− 0.10 to 0.15)
Total prey activity density border structures/focal area	**0.15 (0.02 to 0.30)**
Structural richness	0.06 (− 0.05 to 0.17)
Random effects	**Variance (± SD)**
Deployment (intercept)	0.17 (± 0.41)
Total prey activity density intensive grassland/focal area (slope)	0.19 (± 0.44)
Total prey activity density extensive grassland/focal area (slope)	0.09 (± 0.30)
Total prey activity density biodiv. structures/focal area (slope)	0.11 (± 0.34)
Total prey activity density crop rotation/focal area (slope)	0.20 (± 0.45)
Total prey activity density border structures/focal area (slope)	0.38 (± 0.62)
Structural diversity	0.17 (± 0.41)

We present the mean estimates of β and associated 95% credible interval of the posterior distribution of a logistic mixed effect model based on 65 individuals. Sex, structural richness, and total prey activity density per habitat category and focal area were introduced as explanatory variables, tag deployment as random intercept, and total prey activity density per habitat category and focal area as random slopes

Effects whose credible interval does not include 0 are shown in bold

biodiversity structures were avoided. (RSS: 0.79, CrI: 0.71 to 0.88).

Discussion

For a comprehensive picture of the ecology of a species, all phases of its life cycle should be studied. While many studies investigate habitat selection during the breeding period, fewer investigate the non-breeding period [1]. In this study we showed that small mammal distribution in different habitats varies over the annual cycle, with a general shift from annual crop-rotation to perennial habitats, which affects the availability of prey for predators and consequently the preference of their hunting grounds. Breeding and non-breeding home-range size were similar, but there was a small shift in the location of home-ranges which was more pronounced in females than males. The changes in prey activity density led to a mainly grassland-oriented habitat selection during the non-breeding period. Furthermore, our results showed the importance of biodiversity promotion areas and border structures within the intensively managed agricultural landscape.

Home range size, location, and composition

With an average size of 6.8 km^2 barn owl non-breeding home range size was similar to its breeding home range size and comparable to breeding home range sizes found in previous studies [44, 45, 58, 61]. Overall, females had larger home ranges than males in both periods. During breeding, home ranges of both sexes are closely bound to the breeding nest box, while the distance enlarged for females but not for males during non-breeding period. Overlap of breeding and non-breeding home range was higher for males than for females, indicating a shift in spatial placement of the home ranges during the non-breeding period in females. Such a pattern could emerge through a difference in nest site fidelity of the sexes during the non-breeding period. Previous studies have shown that in case of divorce (change of partner between years), males stay at the original nest site while almost all females change their nest site [62]. Our data showed a similar pattern, as females were more prone to change the nest site between breeding periods. Additionally, own, unpublished data suggests that males visit nest boxes more frequently and regularly than females outside the reproductive period. These findings together indicate that males exhibit higher nest site fidelity, resulting in regular visits to their nest box during the non-breeding period. That breeding site fidelity is more pronounced in males than in females has been shown for several migratory and non-migratory birds of prey species [63–65]. In contrast, little is known about site fidelity outside the breeding season. Our findings indicate that it may be advantageous for males to be present at the future breeding site early in the year. As a result of this behaviour, they may be more regionally bound and therefore less flexible to explore the surrounding areas during the non-breeding period. That site fidelity during the non-breeding season leads to less flexibility in space use but might lead to competitive advantage for breeding sites in spring has also been demonstrated for common kestrels [66]. Habitat composition of home-ranges is similar between the non-breeding (Fig. 2) and breeding period [44], with crop rotation covering the largest proportion of area. This is less surprising as farmers in our study area rarely change the area planted to a particular crop, but rather the field where they plant the crop.

Habitat selection

Our data suggested the following decreasing order in habitat preference during non-breeding period: urban area > intensive grassland > extensive grassland > crop rotation > forest (Fig. 3). The reasons for such a strong selection towards urban area cannot be entirely answered in the frame of this study, but we formulate two hypotheses. First, owls roosting in buildings can save energy compared to roosting in trees especially in cold periods [67]. During the non-breeding period the pressure to save energy might be especially high, resulting in prolonged roosting behaviour during the night and thus select locations dominated by urban area. Even though baseline energy demand is higher during the non-breeding period, owls need less prey items, as they only need to feed themselves. As catching fewer prey might be less time-consuming, there would be more time available to roost. Second, microstructures around houses, such as gardens, hedges, or small orchards, might be suitable habitats of sufficient size for hunting during the non-breeding period. Being close to buildings and thus less exposed to weather conditions compared to hunting in open area might further favour this behaviour during periods of rough weather. However, as our data does not have the necessary resolution to allow to distinguish between roosting and active hunting behaviour, these two hypotheses remain untested.

The selection of intensive grassland (Fig. 3) is not very surprising, as previous studies showed that different types of grassland (pastures or meadows, intensively or extensively managed) are preferred by birds of prey during breeding [9, 44, 68, 69] and our analysis showed that for barn owls this preference seems to persist into the non-breeding period. Even though we see a positive selection of extensive grassland compared to crop rotation, the effect is very weak, which could be partly explained by the scarcity of these structures within the landscape (rareness effect). Further, the presence of biodiversity structures (hedges, trees, wildflower strips, rotational fallows) seemed to positively influence selection of grassland dominated areas (Fig. 3). This effect was pronounced in extensive grassland dominated areas and weaker in intensive grassland. However, the presence of biodiversity structures does not seem to influence the selection of the other habitat categories. Again, there are different explanations. While grasslands may provide suitable habitat for hunting, the neighbouring biodiversity structures could provide perching opportunities, allowing raptors to use a sit-and-wait hunting strategy instead of hunting on the wing [70]. Our own, but yet unpublished data suggest that hunting success in barn owls is higher if owls hunt from perches compared to hunting on the wings, possibly leading to a strong selection towards perch hunting in periods with high energetic baseline needs such as the colder non-breeding period [70–72]. Another possibility is that nearby biodiversity structures could cause a spillover of small mammals into adjacent grasslands. Previous studies showed that semi natural habitats harbour high density of small mammals and can indeed act as a refuge and even as a source for reuse or recolonisation of intensively managed area in spring and summer [14, 15, 17, 18, 23–25, 27, 73].

Area dedicated to crop rotation, which represents the most abundant habitat category within the home ranges of our birds, showed a lower selection compared to intensive grasslands (Fig. 3). Crop rotations, especially cereal fields, are used by birds of prey during the breeding period [9, 44, 74, 75], however crop rotations fields look totally different in terms of vegetation coverage and food availability during the non-breeding period. In our analysis we did not find any preference for crop-rotations (cereal, colza, catch crop, maize, sugar-beet) over grassland during the non-breeding period. We also showed that small mammal activity density in crop-rotations drops drastically in late summer. This drop is most probably induced by harvesting which has been shown to affect small mammal populations either directly due to mortality caused by the harvesters, or due to a change in habitat suitability (reduced cover and food availability) for small mammals [14, 15, 18, 76]. While birds of prey benefit from the increased availability of prey in crop rotation fields during the breeding period, this effect may only persist until shortly after harvest when this habitat instantly become unattractive for small mammals and thus also for their predators.

Habitat selection, biodiversity structures and prey

We showed that biodiversity structures (such as hedges, single trees, wildflower strips and rotational fallows) boost the preference for grassland dominated areas during the non-breeding period. This could be either due to an elevated abundance of perching opportunities when biodiversity structures are present, or due to high prey availability within these structures. We thus investigated whether habitat selection varies depending on prey activity density and the presence or absence of biodiversity structures (Fig. 4). We found a preference for areas with a high vole activity density within the focal area, which was even stronger when biodiversity structures were present. For small mammal activity density, the presence of biodiversity structures has a small opposite effect. Knowing that the two methods used in the small mammal monitoring represent a different spectrum of prey species, there are different possible explanations for the observed results.

The vole activity density represents almost exclusively the availability (presence, activity) of *Microtus* and *Arvicola* species (~70% of barn owl prey, [36]). Selection for focal areas with a high vole activity density may be due to the altered accessibility of this prey type during the non-breeding period (Fig. 4). High, dense, and fast re-growing vegetation is thought to limit prey accessibility during the breeding period [9, 38, 68] but this might change later in the year. Indeed, the increase in vole signs observed from the breeding to the non-breeding period doesn't solely represent an increase in vole abundance and activity but also partially reflects increased visibility of the signs for the observer during non-breeding period. While the signs, and therefore also voles themselves, are often hidden in long and dense vegetation during summer, they are more visible to the human eye and therefore also more accessible to the predator during the non-breeding period. Even though voles might be more accessible in the non-breeding than in the breeding period, hunting them during the non-breeding period could be quite time and energy consuming given that voles lead a rather secretive life and low temperatures and decreased vegetation cover further reduce vole activity [76, 77]. Nevertheless, hunting in areas with high vole activity density could be the most lucrative option during the non-breeding period, and perch hunting could be energetically beneficial. Grassland can provide high vole activity density, while the presence of biodiversity structures can provide the needed perching opportunities. Perching opportunities, especially small woody features, are crucial for the exploitation of agricultural landscapes by diurnal raptors [78] and their importance can even vary between periods. Studies on hunting behaviour of common kestrel have demonstrated a switch from use of hunting on the wing during summer, to perch hunting during winter [71, 72]. The observed habitat selection pattern may indicate that a similar, period specific, change in hunting behaviour also occurs in barn owls, but this remains to be tested.

Small mammal activity density represents the aboveground movements of a wide range of prey species, tending to include more mobile and active prey species such as the wood mice (home range: 4900 up to 14,400 m^2, [18]). Consequently, the selection strength with regard to the activity density of small mammals also shows different patterns than with regard to the activity density of voles. While the presence of biodiversity structures seems beneficial at low small mammal activity density within focal areas, the positive effect of the structures vanishes towards higher activity densities (Fig. 4). The overall lower impact on focal area selection of small mammal activity density compared to vole activity density could result from the seasonal shift of prey availability. While small mammal activity density tended to be high among different habitat categories and especially in crop-rotation during the breeding period, this pattern changes during the non-breeding period. In agreement with previous studies on different small mammal species [14, 15, 17, 18] we observe a decrease inactivity density within crop plantations after harvest. Prey availability in crop-rotation dominated areas drops and activity only remains high in habitats which are unsuitable for hunting (forests).

Looking at the different foraging habitat categories separately, we see that focal areas with high total prey activity densities within grasslands and border structures get selected (Table 3). As we already know that owls prefer focal areas dominated by intensive grassland and areas with high vole activity density, the selection of focal areas with high prey activity density within intensive and extensive grassland is thus consistent with the previous findings. This further strengthens our conclusion that especially grasslands provide crucial food sources during the non-breeding period. The preference for focal areas with high total activity density in border structures is quite interesting as these structures usually only cover small areas within focal areas. That border structures are attractive habitat for voles [26] and consequently attract birds of prey has already been shown for little owls, common buzzards, common kestrels and black kites [38, 70]. The preference for border structures could be a combination of two effects: firstly, an increased availability of prey within border structures, and secondly, the fact that they are often found next to roads equipped with road sings and poles. These poles and road signs can serve as perches and could have a similar effect on selection as we hypothesized for the presence of biodiversity structures, by saving energy through perch hunting [70, 72]. The negative effect of high prey availability in biodiversity structures may seem contradictory at first. However not only prey abundance but also its accessibility is important for the selection of certain habitat structures [9, 38, 68]. Thus, a high total prey activity density per se does not necessarily favour selection, as these prey items are not necessarily accessible and can only be reached at the edge of these structures, or when they migrate into the adjacent grassland [38, 68].

Conclusions

Our study highlights the need to investigate the full annual cycle to identify period-specific changes in animals' behaviour ecology. During the non-breeding period owls showed a strong selection towards areas dominated by urban area, which are likely used for roosting. The patchier prey distribution during the non-breeding compared to the breeding period led to habitat selection towards grassland, which may mean that the ongoing conversion of permanent grasslands to crop rotation fields in Europe [79] could influence the demography of the species. While such a shift might only have moderate impacts on survival and reproduction during the breeding period, when prey is available within crop rotation, the decrease of grasslands could negatively affect survival during the non-breeding period due to shortage of prey. Biodiversity promotion areas, which have been shown to be an important driver of habitat selection during the breeding [44] and the non-breeding period, are mainly important as refuge and source habitat of small mammals [16, 23–25] but might be of limited suitability as direct hunting grounds for birds of prey [9, 38]. On the other hand, the woody structures within biodiversity promotion areas might serve as perching opportunities to facilitate hunting. Therefore, the distribution of such biodiversity promotion areas within the landscapes is of utmost importance for effective conservation measures. We therefore conclude that to effectively conserve birds preying on small mammals within the intensively managed landscape, we need to maintain and promote a diverse agricultural landscape interspersed with biodiversity promotion areas close to preferred hunting habitats. Future analyses should cover the effects breeding and non-breeding habitat composition and corresponding prey availability on survival and reproduction. Furthermore, it would be interesting to investigate whether conspecifics influence habitat selection. The density of animals using a particular habitat can influence the habitat selection decision of other individuals [80]. Given the large fluctuations that barn owl populations can undergo in temperate regions, the influence of density on habitat selection could vary greatly from year to year and over the course of a year.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-023-00376-3.

Additional file1: S1.1: Small mammal sampling regions. S1.2: Small mammal sampling design visualization. S1.3: Information extraction from the federal layer TLM3D. S1.4: Information extraction from cantonal layers on agricultural fields. S1.5: Merged habitat types for habitat categories. S2.1: Model validations. S2.2: Small mammal activity density. S2.3: Vole activity density. S2.4: Models home range. S2.5: Model distance centroid nest box.

Acknowledgements
We thank all the field assistants for their tremendous help in organising the field work and collecting the data. R. Spaar, M. Grübler and S. Jenni-Eiermann for their support in developping the project and K. Meichtry-Stier and Florian Orgeret for inputs on the analysis. We would also like to thank the two anonymous reviewers and Burt Kotler for their valuable comments on an earlier version, which enabled us to further improve the manuscript.

Author contributions
All authors designed the project, AR and BA funded the research. RB, RS and KS collected data. RB and BA analysed data. RB wrote the manuscript, with significant contributions of all co-authors. All authors read and approved the final manuscript.

Funding
Open access funding provided by Swiss Ornithological Institute and University of Lausanne

Availability of data and materials
Datasets and the R script to reproduce the resource selection functions, as well as their validations, are available under: https://doi.org/10.5281/zenodo.7664853. The GPS data are stored in Movebank (www.movebank.org), under the project named "Barn owl Winter" (ID 1433219445) and are available on reasonable request. The habitats maps produced during the study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
This study meets the legal requirements of capturing, handling, and attaching GPS devices to barn owls in Switzerland (legal authorizations: VD and FR 2844 and 3213; capture and ringing permissions from the Federal Office for the Environment).

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland. [2]Department of Ecology and Evolution, University of Lausanne, Building Biophore, 1015 Lausanne, Switzerland. [3]Agroecology and Environment, Agroscope, Reckenholzstrasse 191, 8046 Zurich, Switzerland.

Received: 24 August 2022 **Accepted:** 16 February 2023

References

1. Marra P, Cohen E, Loss S, Rutter J, Tonra C. A call for full annual cycle research in animal ecology. Biol Lett. 2015. https://doi.org/10.1098/rsbl.2015.0552.
2. Norrdahl K, Klemola T, Korpimäki E, Norrdahl MK, Klemola K, Korpimäki T, et al. Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. Oikos. 2002;99:419–30. https://doi.org/10.1034/j.1600-0706.2002.12025.x.
3. Veľký M, Kaňuch P, Krištín A. Food composition of wintering great tits (Parus major): habitat and seasonal aspects. Folia Zool. 2011;60:228–36. https://doi.org/10.25225/fozo.v60.i3.a7.2011.
4. Panzeri M, Menchetti M, Mori E. Habitat use and diet of the *Eurasian scops* owl *Otus scops* in the breeding and wintering periods in Central Italy. Ardeola Spanish Soc Ornithol. 2014;61:393–9. https://doi.org/10.13157/arla.61.2.2014.393.
5. Newton I. Population limitation in birds. Academic Press; 1998.
6. Kostrzewa R, Kostrzewa A. Winter weather, spring and summer density, and subsequent breeding success of Eurasian Kestrels, Common Buzzards, and Northern Goshawks. Auk Narnia. 1991;108:342–7. https://doi.org/10.1093/auk/108.2.342.
7. Karell P, Ahola K, Karstinen T, Zolei A, Brommer JE. Population dynamics in a cyclic environment. J Anim Ecol. 2009;78:1050–62. https://doi.org/10.1111/j.1365-2656.2009.01563.x.
8. Siriwardena GM, Calbarde NA, Vickery JA. Farmland birds and late winter food. Ibis. 2008;150:585–95. https://doi.org/10.1111/j.1474-919X.2008.00828.x.
9. Arlettaz R, Krähenbühl M, Almasi B, Roulin A, Schaub M. Wildflower areas within revitalized agricultural matrices boost small mammal populations but not breeding Barn Owls. J Ornithol. 2010;151:553–64. https://doi.org/10.1007/s10336-009-0485-0.
10. Solonen T, Ahola K, Karstinen T. Clutch size of a vole-eating bird of prey as an indicator of vole abundance. Environ Monit Assess. 2015. https://doi.org/10.1007/s10661-015-4783-0.
11. Huitu O, Koivula M, Korpimäki E, Klemola T, Norrdahl K. Winter food supply limits growth of northern vole populations in the absence of predation. Ecology. 2003;84:2108–18. https://doi.org/10.1890/02-0040.
12. Huitu O, Norrdahl K, Korpimäki E. Landscape effects on temporal and spatial properties of vole population fluctuations. Oecologia. 2003;135:209–20. https://doi.org/10.1007/s00442-002-1171-6.
13. Tkadlec E, Zejda J. Small rodent population fluctuations: the effects of age structure and seasonality. Evol Ecol. 1998;12:191–210. https://doi.org/10.1023/A:100658371304.
14. Tew TE, Macdonald DW. The effects of harvest on arable wood mice *Apodemus sylvaticus*. Biol Conserv. 1993. https://doi.org/10.1016/0006-3207(93)90060-E.
15. Jacob J. Short-term effects of farming practices on populations of common voles. Agric Ecosyst Environ. 2003;95:321–5. https://doi.org/10.1016/S0167-8809(02)00084-1.
16. Heroldová M, Bryja J, Zejda J, Tkadlec E. Structure and diversity of small mammal communities in agriculture landscape. Agric Ecosyst Environ. 2007;120:206–10. https://doi.org/10.1016/j.agee.2006.09.007.
17. Tattersall FH, Macdonald DW, Hart BJ, Manley WJ, Feber RE. Habitat use by wood mice (*Apodemus sylvaticus*) in a changeable arable landscape. J Zool. 2001;255:487–94. https://doi.org/10.1017/S095283690100156X.
18. Todd IA, Tew TE, Macdonald DW. Arable habitat use by wood mice (*Apodemus sylvaticus*): 1: macrohabitat. J Zool. 2000;250:299–303. https://doi.org/10.1111/j.1469-7998.2000.tb00773.x.
19. Jacob J, Hempel N. Effects of farming practices on spatial behaviour of common voles. J Ethol. 2003;21:45–50. https://doi.org/10.1007/s10164-002-0073-8.
20. Preston CR. Distribution of raptor foraging in relation to prey biomass and habitat structure. Condor. 1990;92:107–12. https://doi.org/10.2307/1368388.
21. Tew TE, Todd IA, Macdonald DW. Arable habitat use by wood mice (*Apodemus sylvaticus*): 2: microhabitat. J Zool. 2006. https://doi.org/10.1111/j.1469-7998.2000.tb00774.x.
22. Macdonald DW, Tew TE, Todd IA, Garner JP, Johnson PJ. Arable habitat use by wood mice (*Apodemus sylvaticus*): 3: a farm-scale experiment on the effects of crop rotation. J Zool. 2000;250:313–20. https://doi.org/10.1111/j.1469-7998.2000.tb00775.x.
23. Janova E, Heroldová M. Response of small mammals to variable agricultural landscapes in Central Europe. Mamm Biol. 2016;81:488–93. https://doi.org/10.1016/j.mambio.2016.06.004.
24. Fischer C, Thies C, Tscharntke T. Small mammals in agricultural landscapes: opposing responses to farming practices and landscape complexity. Biol Conserv. 2011;144:1130–6. https://doi.org/10.1016/j.biocon.2010.12.032.
25. Fischer C, Schröder B. Predicting spatial and temporal habitat use of rodents in a highly intensive agricultural area. Agric Ecosyst Environ. 2014;189:145–53. https://doi.org/10.1016/j.agee.2014.03.039.
26. Rodríguez-Pastor R, Luque-Larena JJ, Lambin X, Mougeot F. "Living on the edge": the role of field margins for common vole (*Microtus arvalis*) populations in recently colonised Mediterranean farmland. Agric Ecosyst Environ. 2016;231:206–17. https://doi.org/10.1016/j.agee.2016.06.041.
27. Jacob J, Manson P, Barfknecht R, Fredricks T. Common vole (*Microtus arvalis*) ecology and management: implications for risk assessment of plant protection products. Pest Manag Sci. 2014;70:869–78. https://doi.org/10.1002/ps.3695.

28. Klok C, Roos AM. Effects of vole fluctuations on the population dynamics of the barn owl *Tyto alba*. Acta Biotheor. 2007;55:227–41. https://doi.org/10.1007/s10441-007-9013-x.
29. Altwegg R, Roulin A, Kestenholz M, Jenni L. Demographic effects of extreme winter weather in the barn owl. Oecologia. 2006;149:44–51.
30. Massemin S, Handrich Y. Higher winter mortality of the barn owl compared to the long-eared owl and the tawny owl. Condor. 1997;99:969. https://doi.org/10.2307/1370148.
31. Thouzeau C, Duchamp C, Handrich Y. Energy metabolism and body temperature of barn owls fasting in the cold. Physiol Biochem Zool. 2015;72:170–8. https://doi.org/10.1086/316659.
32. Keller V, Gerber A, Schmid H, Volet B, Zbinden N. Rote Liste Brutvögel. Umwelt-Vollzug Nr. 1019, 53 P. Bern, Sempach: Bundesamt für Umwelt and Schweizerische Vogelwarte Sempach; 2010.
33. Bruijn O. Ecology and conservation of the barn owl in farmland habitats in Liemers and Achterhoek (The Netherlands). Ardea. 1994;82:1–109.
34. Frey C, Sonnay C, Dreiss A, Roulin A. Habitat, breeding performance, diet and individual age in Swiss Barn Owls (*Tyto alba*). J Ornithol. 2010;152:279–90. https://doi.org/10.1007/s10336-010-0579-8.
35. Béziers P, Roulin A. Double brooding and offspring desertion in the barn owl *Tyto alba*. J Avian Biol. 2016;47:235–44. https://doi.org/10.1111/jav.00800.
36. Roulin A. The function of food stores in bird nests: observations and experiments in the Barn Owl Tyto alba. Ardea. 2004;92:69–78.
37. Fichet-Calvet E, Pradier B, Quéré JP, Giraudoux P, Delattre P. Landscape composition and vole outbreaks: evidence from an eight year study of *Arvicola terrestris*. Ecography. 2000;23:659–68. https://doi.org/10.1111/j.1600-0587.2000.tb00309.x.
38. Apolloni N, Grüebler MU, Arlettaz R, Gottschalk TK, Naef-Daenzer B. Habitat selection and range use of little owls in relation to habitat patterns at three spatial scales. Anim Conserv. 2017;65:210. https://doi.org/10.1111/acv.12361.
39. Hansson L. Field signs as indicators of vole abundance. J Appl Ecol. 1979;16:339.
40. Glennon MJ, Porter WF, Demers CL. An alternative field technique for estimating diversity of small-mammal populations. J Mammal. 2002;83:734–42. https://doi.org/10.1644/1545-1542(2002)083%3c0734:AAFTFE%3e2.0.CO;2.
41. Jareño D, Viñuela J, Luque-Larena JJ, Arroyo L, Arroyo B, Mougeot F. A comparison of methods for estimating common vole (*Microtus arvalis*) abundance in agricultural habitats. Ecol Indic. 2014;36:111–9.
42. Embar K, Mukherjee S, Kotler BP. What do predators really want? The role of gerbil energetic state in determining prey choice by Barn Owls. Ecology. 2014;95:280–5. https://doi.org/10.1890/13-0836.1.
43. Fay R, Michler S, Laesser J, Jeanmonod J, Schaub M. Large-scale vole population synchrony in central Europe revealed by kestrel breeding performance. Front Ecol Evol. 2020;7:512.
44. Séchaud R, Schalcher K, Machado AP, Almasi B, Massa C, Safi K, et al. Behaviour-specific habitat selection patterns of breeding barn owls. Mov Ecol BioMed Central. 2021;9:1–11. https://doi.org/10.1186/s40462-021-00258-6.
45. Séchaud R, Schalcher K, Almasi B, Bühler R, Safi K, Romano A, et al. Home range size and habitat quality affect breeding success but not parental investment in barn owl males. Sci Rep. 2022;12:1–11. https://doi.org/10.1038/s41598-022-10324-7.
46. Kranstauber B, Smolla M, Scharf AK. Move: visualizing and analyzing animal track data. R-package; 2021.
47. Johnson DH. The comparison of usage and availability measurements for evaluating resource preference. Ecology. 1980;61:65–71. https://doi.org/10.2307/1937156.
48. Wood S. Mixed GAM computation vehicle with automatic smoothness estimation. R-package; 2022.
49. Gabry J, Veen D, Stan development team, Andreae M, Betancourt M, Carpenter B, et al. Shinystan: interactive visual and numerical diagnostics and posterior analysis for Bayesian Models. R-package; 2022.
50. Lüdecke D, Makowski D, Ben-Shachar M, Patil I, Højsgaard S, Wiernik B, et al. Parameters: processing of model parameters. R-package; 2021.
51. Manly BFJ. Resource selection by animals. 2nd ed. Dordrecht: Kluwer; 2002.
52. Brooks M, Bolker B, Kristensen K, Maechler M, Magnusson A, McGillycuddy M, et al. glmmTMB: Generalized linear mixed models using template model builder. R package; 2022.
53. Gillies C, Hebblewhite M, Nielsen S, Krawchuk M, Aldrige C, Frair J, et al. Application of random effects to the study of resource selection by animals. J Anim Ecol. 2006;75:887–98. https://doi.org/10.1111/j.1365-2656.2006.01106.x.
54. Muff S, Signer J, Fieberg J. Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects models using Bayesian or frequentist computation. J Anim Ecol. 2020;89:80–92. https://doi.org/10.1111/1365-2656.13087.
55. Warton DI, Shepherd LC. Poisson point process models solve the "pseudo-absence problem" for presence-only data in ecology. Ann Appl Stat. 2010. https://doi.org/10.1214/10-aoas331.
56. Fieberg J, Signer J, Smith B, Avgar T. A 'How to' guide for interpreting parameters in habitat-selection analyses. J Anim Ecol. 2021;90:1027–43. https://doi.org/10.1111/1365-2656.13441.
57. Avgar T, Lele SR, Keim JL, Boyce MS. Relative selection strength: quantifying effect size in habitat- and step-selection inference. Ecol Evol. 2017;7:5322–30. https://doi.org/10.1002/ece3.3122.
58. Taylor IR. Barn owls. 1st ed. Cambridge: Cambridge University Press; 1994.
59. Johnson CJ, Nielsen SE, Merrill EH, Mcdonald TL, Boyce MS. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. J Wildlife Manag. 2006;70:347–57. https://doi.org/10.2193/0022-541X(2006)70[347:RSFBOU]2.0.CO;2.
60. R Development Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2021.
61. Almasi B, Roulin A, Jenni L. Corticosterone shifts reproductive behaviour towards self-maintenance in the barn owl and is linked to melanin-based coloration in females. Horm Behav. 2013;64:161–71. https://doi.org/10.1016/j.yhbeh.2013.03.001.
62. Dreiss AN, Roulin A. Divorce in the barn owl: securing a compatible or better mate entails the cost of re-pairing with a less ornamented female mate. J Evol Biol. 2014;27:1114–24. https://doi.org/10.1111/jeb.12402.
63. Newton I, Wyllie I. Fidelity to nesting territory among european sparrowhawks in three areas. Raptor Res. 1992;26:108–14.
64. Linkhart BD, Reynolds RT. Return rate, fidelity, and dispersal in a breeding population of Flammulated Owls (Otus Flammeolus). Auk. 2007;124:264–75.
65. Miller KE, Smallwood JA. Breeding-site fidelity of Southeastern American Kestrels (*Falco sparverius* paulus). Raptor Res Found. 2009;43:369–71. https://doi.org/10.3356/JRR-08-661.
66. Riegert J, Fuchs R. Fidelity to Roost Sites and Diet Composition of Wintering Male Urban Common Kestrels Falco tinnunculus. Museum and Institute of Zoology, Polish Academy of Sciences; 2011; 46:183–9. https://doi.org/10.3161/000164511X625955
67. McCafferty DJ, Moncrieff JB, Taylor IR. How much energy do barn owls (*Tyto alba*) save by roosting? J Therm Biol Pergamon. 2001;26:193–203. https://doi.org/10.1016/S0306-4565(00)00042-5.
68. Aschwanden J, Birrer S, Jenni L. Are ecological compensation areas attractive hunting sites for common kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*)? J Ornithol. 2005;146:279–86. https://doi.org/10.1007/s10336-005-0090-9.
69. Garratt CM, Hughes M, Eagle G, Fowler T, Grice PV, Whittingham MJ. Foraging habitat selection by breeding Common Kestrels *Falco tinnunculus* on lowland farmland in England. Bird Stud. 2011;58:90–8. https://doi.org/10.1080/00063657.2010.526192.
70. Meunier FD, Verheyden C, Jouventin P. Use of roadsides by diurnal raptors in agricultural landscapes. Biol Conserv. 2000;92:291–8. https://doi.org/10.1016/S0006-3207(99)00094-4.
71. Masman D, Daan S, Dijkstra C. Time allocation in the kestrel (*Falco tinnunculus*), and the principle of energy minimization. J Anim Ecol. 1988;57:411. https://doi.org/10.2307/4914.
72. Pettifor RA. Seasonal variation, and associated energetic implications, in the hunting behaviour of the Kestrel. Bird Study. 1983;30:201–6. https://doi.org/10.1080/00063658309476797.
73. Aschwanden J, Holzgang O, Jenni L. Importance of ecological compensation areas for small mammals in intensively farmed areas. Wildlife Biol. 2007;13:150–8. https://doi.org/10.2981/0909-6396(2007)13[150:IOECAF]2.0.CO.
74. Assandri G, Cecere JG, Sarà M, Catoni C, de Pascalis F, Morinay J, et al. Context-dependent foraging habitat selection in a farmland raptor along an agricultural intensification gradient. Agric Ecosyst Environ. 2022;326:107782.
75. Cardador L, Carrete M, Mañosa S. Can intensive agricultural landscapes favour some raptor species? The Marsh harrier in north-eastern Spain. Anim Conserv. 2011;14:382–90. https://doi.org/10.1111/j.1469-1795.2011.00449.x.

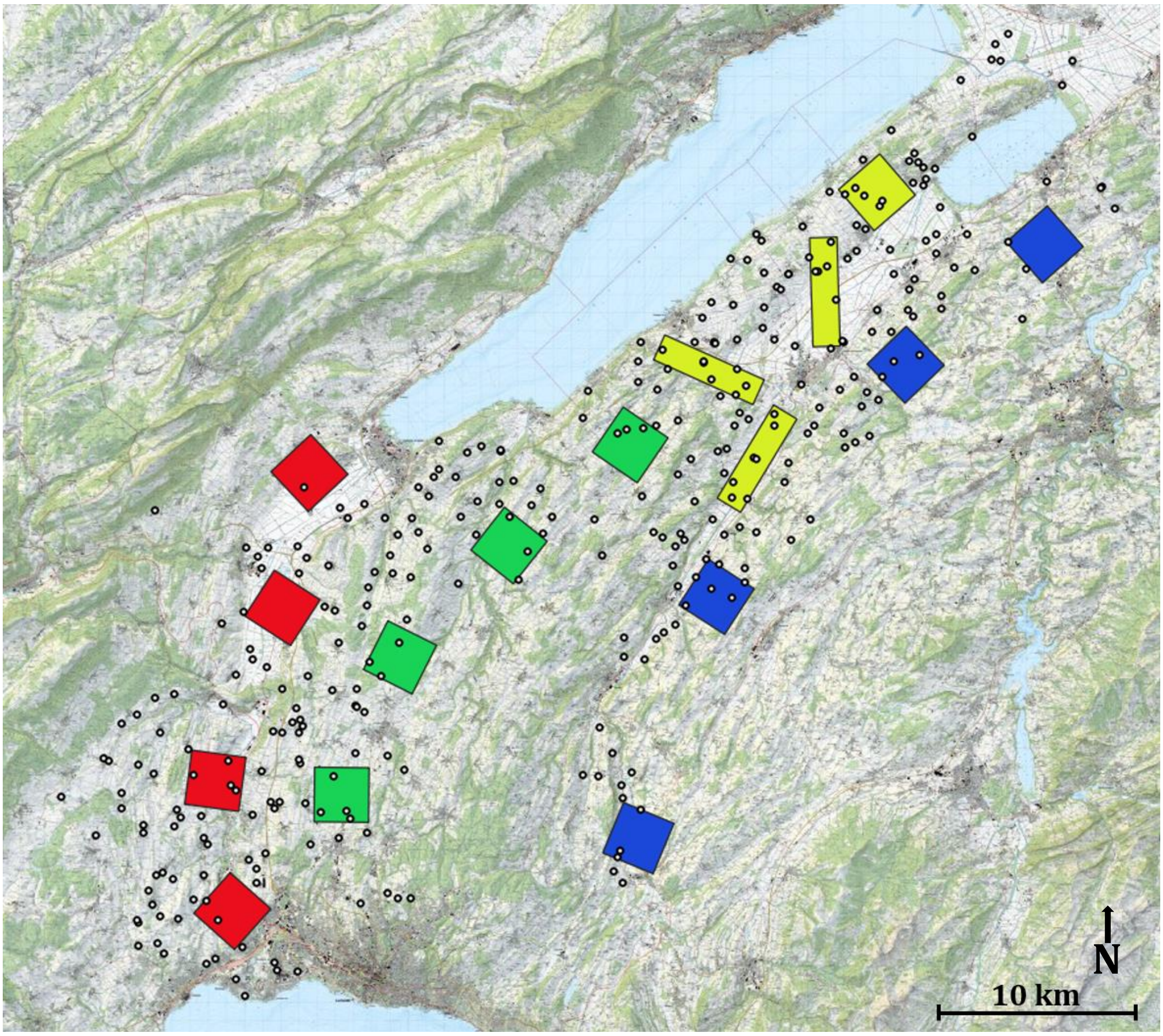
76. Jacob J. Response of small rodents to manipulations of vegetation height in agro-ecosystems. Integr Zool. 2008;3:3–10. https://doi.org/10.1111/j.1749-4877.2008.00078.x.
77. Hoogenboom I, Daan S, Dallinga JH, Schoenmakers M. Seasonal change in the daily timing of behaviour of the common vole. Microtus Arvalis Oecol Oecol. 1984;61:18–31. https://doi.org/10.1007/BF00379084.
78. Mirski P, Väli Ü. Movements of birds of prey reveal the importance of tree lines, small woods and forest edges in agricultural landscapes. Landsc Ecol. 2021;36:1409–21. https://doi.org/10.1007/s10980-021-01223-9.
79. Stoate C, Báldi A, Beja P, Boatman ND, Herzon I, van Doorn A, et al. Ecological impacts of early 21st century agricultural change in Europe: a review. J Environ Manag Acad Press. 2009;91:22–46. https://doi.org/10.1016/j.jenvman.2009.07.005.
80. Fretwell SD, Lucas HL. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 1969;19:16–36. https://doi.org/10.1007/BF01601953.

Publisher's Note

Supplementary material Chapter 1:

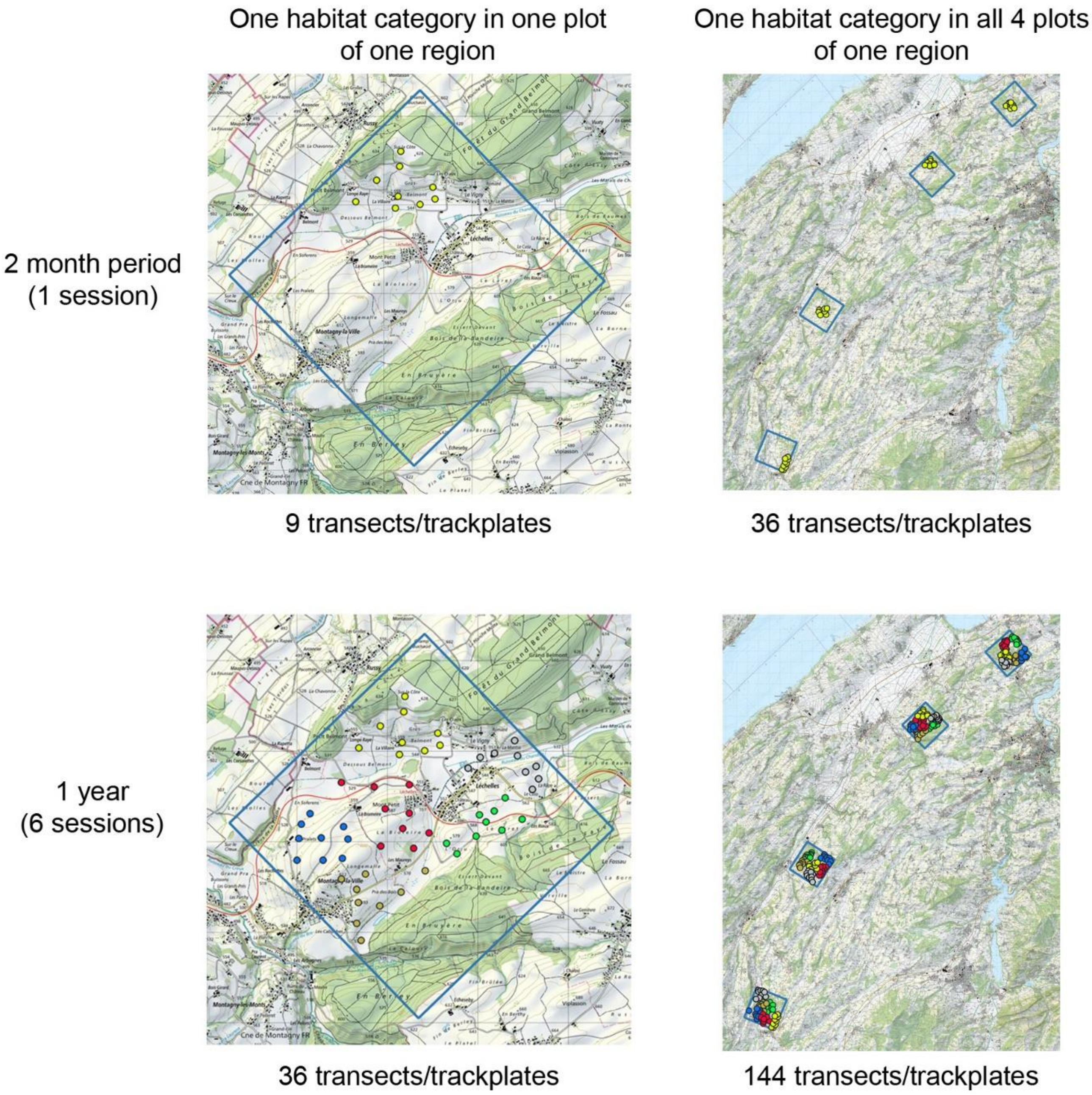
S1.1 Small mammal sampling regions:

Each of the four regions contsist of 4 plots: red: plain of Orbe, yellow: plain of the Broye, blue: Haut-Fribourg and green: Gros de Vaud region. Nest box locations are indicated by points.



S1.2 Small mammal sampling design visualization

Each of the 4 habitat types was sampled with 9 transects/trackplates within each of the 4 plots of one region (upper left and right). This results in 36 transects/trackplates per habitat type per region per 2-month session (upper right). Within the 9 km^2 plots the transects and trackplates were laid that they covered the whole area over the duration of the year which consisted out of 6 sessions (lower left). Over the duration of one year each habitat within each region was sampled by 144 transects/trackplates (lower right).



S1.3 Information extraction from the federal layer TLM3D

Below a table with the extracted categories and their treatment:

TLM 3D category	Buffer	Further treatment
buildings	+ 10 m (mean width)	holes < 500m^2 closed
highway	+ 20 m (mean width)	
motorway	+ 12 m (mean width)	
railway	+ 5 m (mean width)	
10 m street	+ 12 m (mean width)	
8 m street	+ 9.2 m (mean width)	
6 m street	+ 7.2 m (mean width)	
4 m street	+ 5.2 m (mean width)	
2 m path	+ 2.3 m (mean width)	
1 m path	+ 1.5 m (mean width)	
hedges	+ 1 m	
forest	- 3 m	holes < 500m^2 closed
forest edge	+ 7 m around forest	
border structures	+1 m around all streets/railway	

S1.4 Information extraction from cantonal layers on agricultural fields

For all locations in canton Vaud, agricultural land use was available as a GIS-layer from the cantonal authority. For canton Fribourg a layer with information about permanent cultures only was available and we therefore mapped the agricultural land use within an area of 1.5 km (which corresponds to the mean home range used by breeding barn owls [68] around breeding sites of equipped owls during winter. After the GPS modules were recovered, areas of the home ranges which laid outside the already mapped 1.5 km radius were mapped as soon as possible. The information from the cantonal layers was extracted and merged with the data from the habitat mapping. To be able to merge the cantonal layer with the mapped layer we had to bring them to the same resolution and defined the following categories: Intensive grassland, extensive grassland, artificial grassland, intensive pasture, extensive pasture, winter cereal, colza, catch crop, wildflower strips and rotational fallows. As cantonal layers hold information about the culture present during summer of the respective year, we needed to combine the information from two years, according to the sowing time of the culture.

Finally, the different layers from the different sources have been clipped with each other to eliminate overlaying polygons. To fasten the workflow and to be able to efficiently extract the habitat information later in the analysis, the polygon layers have been rasterized on a resolution of 25x25m sized cells. This resolution was chosen according to the accuracy of our tags (mean accuracy: 20 m) and the lowest resolution of our base raster which was 2.5 m.

S1.5 Merged habitat types for habitat categories

Categories were merged according to their similar appearance in the field during the non-breeding period (agricultural fields) or because of strong correlations. Before merging we made sure that the habitat types showed similar selection directions in the raw data (ratio available vs. used)

Habitat category merged	Habitat type	Nb. of crop type (cantonal layers)
intensive grassland	intensive pasture intensive meadow artificial grassland	601/602/613/621/632/698/702/703/704 720/616
extensive grassland	extensive pasture extensive meadow	611/612/634/697/851/852/857/858/622 617/618/625/693/694/930
biodiversity structures	rotational fallows wildflower strips hedges single trees	555/556/557/559/572/904/905/908/998
crop-rotation	winter cereals colza catch crop maize potato sugar beet other	501/502/504/505/506/507/508/509/511 512/513/514/515/516/519/526/527/521 522/523/524/525/528/531/534/535/536 537/538/539/541/542/543/544/545/546 547/548/549/551/553/554/566/567/568 569/573/590/591/574/592/594/595/597 598/631/701/705/706/707/708/709/710 711/712/713/714/715/717/718/719/721 722/725/731/735/797/798/801/803/806 807/808/847/848/897/898/909
forest	forest forest edge	from TLM3D
urban area	buildings paths/streets/roads/railways with buffer 1m	from TLM3D

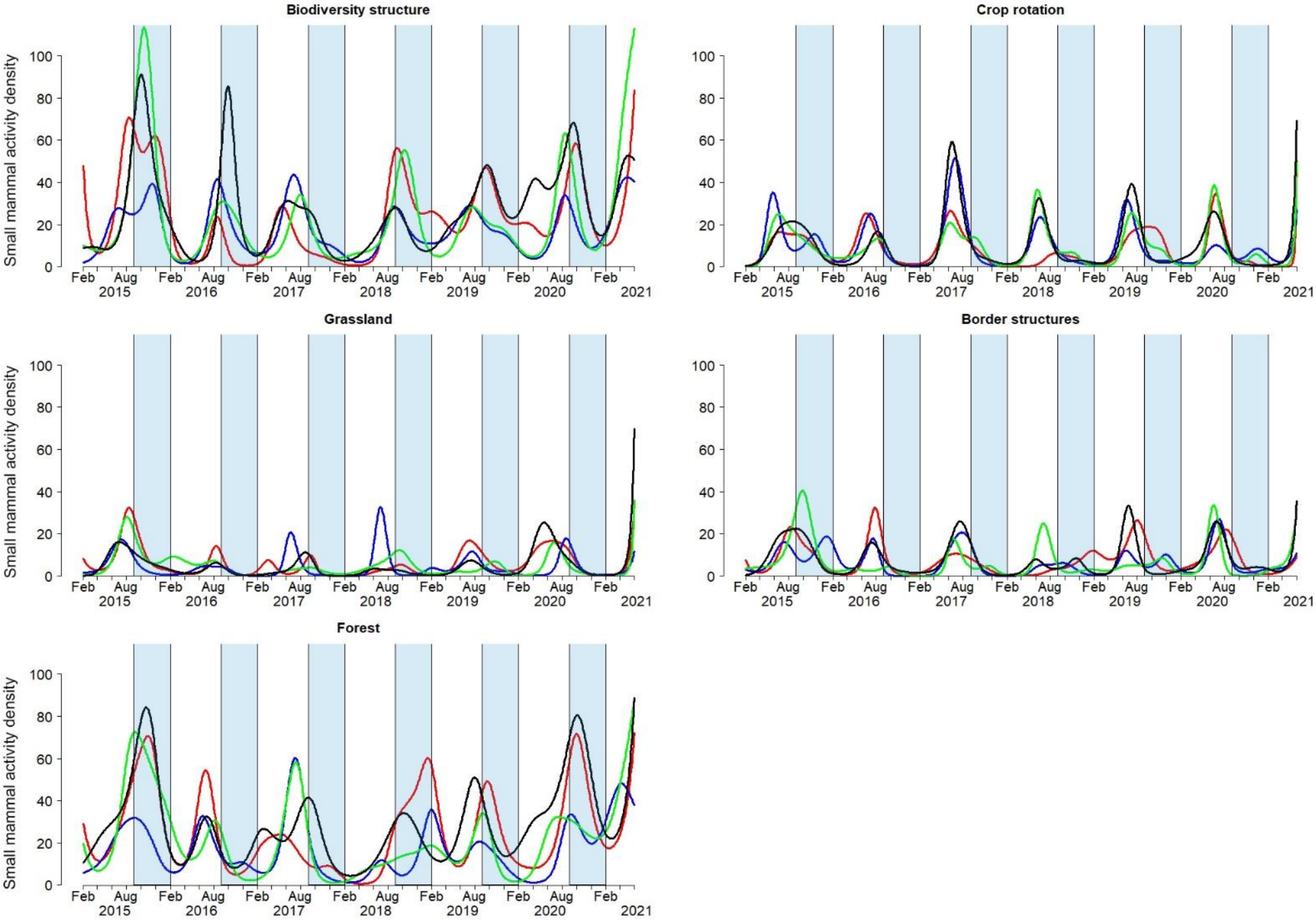
S2.1 Model validations

We separated the dataset into training and test data, by randomly choosing 3 males and 3 females per season (12 individuals test dataset, 58 individuals training dataset). We then run an RSF using the training dataset, extracting the values for relative probability of selection. These values were separated into deciles of about equal size and the expected number of observations was calculated in each bin. To visually inspect the relationship, we plotted the observed number of used locations relative to the expected number in each bin and extracted the slope and intercept of the linear regression laid trough the locations. We repeated the process 10 times and calculated mean slope, intercept, and spearman correlation among the 10 trials as measure for model performance.

Model	Spearman rank corr.	Intercept	Slope	R2
Model dominant habitat category	0.78 (±0.11)	0.03 (±0.02)	0.71 (±0.22)	0.62 (±0.20)
Model dominant habitat category interaction	0.86 (±0.10)	0.03 (±0.02)	0.66 (±0.18)	0.70 (±0.19)
Model total prey activity density	0.80 (±0.11)	0.02 (±0.01)	0.78 (±0.15)	0.72 (±0.23)
Model prey activity density per habitat category	0.71 (±0.15)	0.02 (±0.03)	0.76 (±0.29)	0.41 (±0.26)

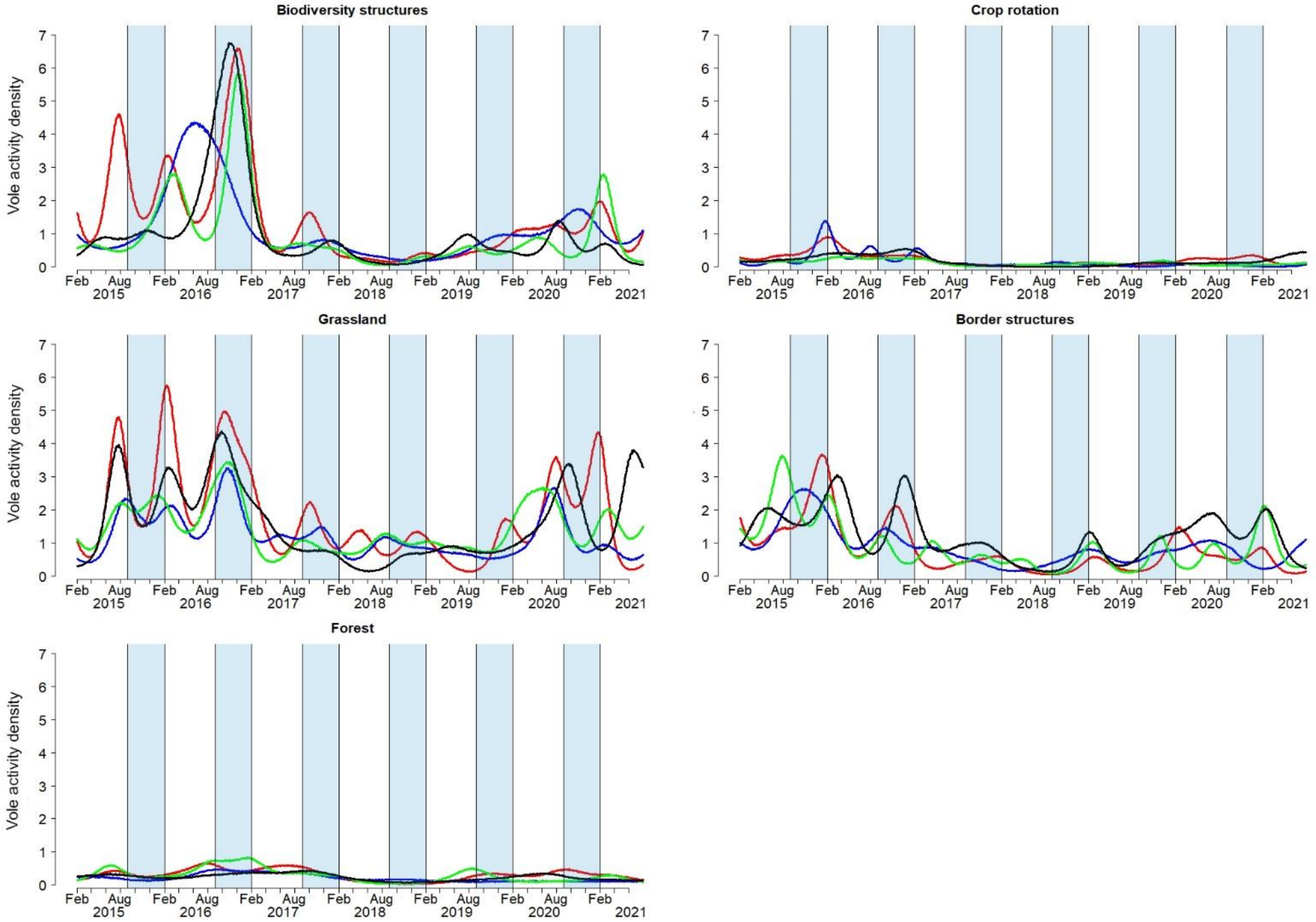
S2.2 Small mammal activity density

Numbers of small mammal traces for track-plates (small-mammal index) were analysed by fitting a generalized additive model. While the total number of traces, on the plates served as response variable, region, observation round, habitat category and temperature were included as explanatory variables. Fitted values for a given time for each habitat structure in each region (red: plain of the Broye, blue: Haut-Fribourg, green: Gros de Vaud, black: plain of Orbe) are estimated and used as an index representing small mammal activity density.



S2.3 Vole activity density

Numbers of vole traces for transects (vole index) were analysed by fitting a generalized additive model. While the total number of traces per transect served as response variable, region, observation round, habitat category and temperature were included as explanatory variables. Fitted values for a given time for each habitat structure in each region (red: plain of the Broye, blue: Haut-Fribourg, green: Gros de Vaud, black: plain of Orbe) are estimated and used as an index representing vole activity density.



S2.4 Models home range

Linear models with log-transformed home range size as response variable and season (breeding/non-breeding), sex and year as explanatory variables. Individual identity was included as random effect. We present the mean estimates of ß and associated 95% credible interval of the posterior distribution based on 51 individuals (27 males, 24 females).

Fixed effects	Main effects ß mean (95%CrI)	With interaction ß mean (95%CrI)
Intercept [log]	2.22 (1.89–2.54)	2.20 (1.86–2.59)
Sex m	**-0.49 (-0.87– -0.14)**	**-0.47 (-0.94– -0.01)**
Season non-breeding	0.10 (-0.13–0.38)	0.11 (-0.24–0.52)
Year	-0.28 (-0.59–0.01)	-0.28 (-0.59–0.05)
Season non-breeding: sex m		0.01 (-0.54–0.52)
Random effects	Variance (±SD)	Variance (±SD)
Individual (Intercept)	0.20 (±0.44)	0.19(±0.44)

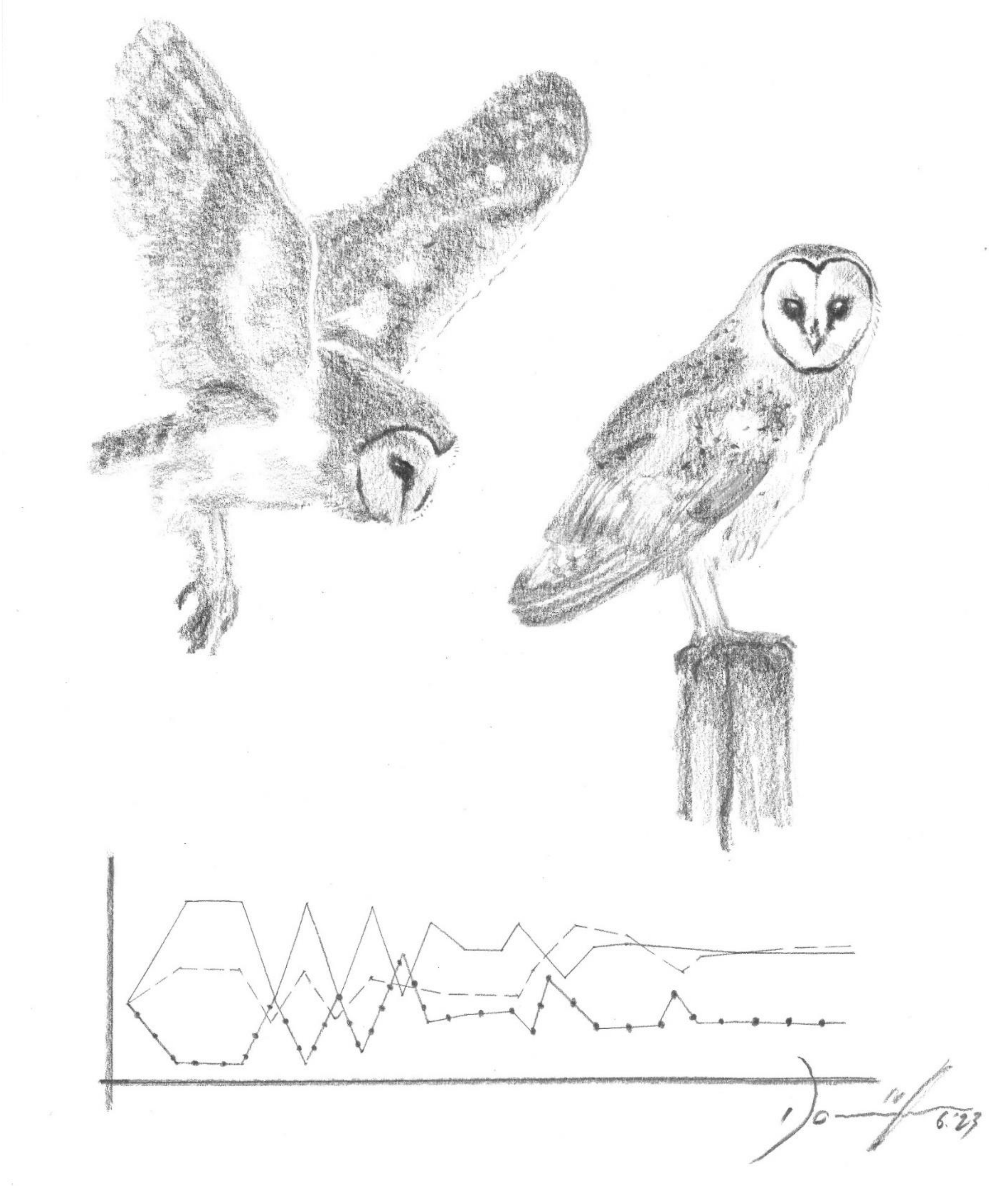
S2.5 Model distance centroid to nest box

We measured: 1) the distance of the centroid of the breeding home range to the breeding nest box (N=46, 24 males, 22 females), 2) the distance of the centroid of the non-breeding home range to the previous breeding nest box (N=51, 27 males, 24 females), 3) the distance of the centroid of the non-breeding home range to the future breeding nest box (N=42, 23 males, 19 females). Linear model with log-transformed distance as response and the type of distance (1,2,3) as well as sex as explanatory variable. Individual and nest box id were included as random effects. We present the mean estimates of ß and associated 95% credible interval of the posterior distribution.

Fixed effects	ß mean (95%CrI)
Intercept [log]	6.36 (5.99–6.81)
Dist. non-breeding -previous nest box	**1.04 (0.63–1.42)**
Dist. non-breeding -future nest box	**1.07 (0.57-1.55)**
Sex m	0.00 (-0.53-0.60)
Dist. non-breeding-previous nest box: sex m	**-0.62 (1.20- -0.07)**
Dist. non-breeding-future nest box: sex m	-0.63 (-1.27-0.00)
Random effects	**Variance (±SD)**
Individual (Intercept)	0.12 (±0.34)
Breeding site: Individual (Intercept)	0.34 (±0.58)

Chapter 2:

Activity patterns covary with sex, plumage coloration and environmental conditions in a nocturnal bird of prey during the non-breeding season



6.'23

Chapter 2

Activity patterns covary with sex, plumage coloration and environmental conditions in a nocturnal bird of prey during the non-breeding season

Roman Bühler[1,2], Paolo Becciu[2], Kim Schalcher[2], Robin Séchaud[1,2], Alexandre Roulin[2] and Bettina Almasi[1]

[1]Swiss Ornithological Institute, Seerose 1, CH-6204, Sempach, Switzerland.

[2]Department of Ecology and Evolution, University of Lausanne, Building Biophore, CH-1015, Lausanne, Switzerland.

Chapter Status:

In preparation. The analyses presented in this chapter will be complemented with additional ones.

Authors contributions:

All authors designed the project, A. R. and B. A. funded the research. R. B. and K. S. collected data. R. B. and B. A. analysed data. R. B. wrote the manuscript, with significant contributions of all co-authors.

Abstract

Animals in temperate regions face temperature fluctuations and changes in trophic productivity. Adapting their behaviour becomes crucial to overcome the energy demands of thermoregulation and the limited resources during colder seasons. By using accelerometer data combined with GPS locations, we investigated the activity patterns of barn owls during the non-breeding period and related them to weather conditions, habitat composition, and prey availability. Our research has shown that the overall activity of barn owls is highest at dusk and dawn, suggesting an adaptation to the main activity period of their prey. Adverse weather conditions (colder temperatures, strong winds, and rain) were associated with a decrease in activity. Activity patterns in barn owls were correlated with prey availability in a habitat specific manner and depended on plumage coloration, most probably due to plumage-coloration specific prey preferences. Our research suggests that owls adapt their foraging behaviour according to prey type (less or more active species) and its availability within the different habitats. These findings have implications for understanding fitness and population dynamics of barn owls, as energy allocation can impact individual fitness which might be especially important during the non-breeding period.

Introduction

Animals living in temperate regions are exposed to environments where temperature and trophic productivity vary dramatically throughout the year. Colder temperatures in autumn and winter increase the amount of energy required for thermoregulation [1,2] while negatively affecting primary producers and consequently the availability of resources for their consumers [1,3]. The extent to which individuals can adapt their foraging strategy is therefore of vital importance in coping with the challenges of the colder season. Nonetheless relatively few studies investigated this period [4].

The optimal foraging theory states that individuals should decrease energy expenditure during foraging to a minimum, while at the same time maximising energy intake [5,6]. To optimize foraging may be of particular importance during the colder non-breeding period. Sedentary birds in temperate regions have demonstrated their ability to adapt their foraging behaviour by either altering their diet [7,8] or shifting their foraging habitat [9]. Birds of prey have been shown to transition from the more energy-intensive flight hunting to the less demanding perch hunting behaviour during colder seasons [10–12]. Similarly, cormorants (*Phalacrocorax carbo*) reduce the time they spend exposed to cold water to decrease the energy costs associated with thermoregulation [13].

When foraging, individuals can maximise their fitness by either minimising the time they spend gathering a given amount of energy (time minimisers) or maximising the net energy intake for a given amount of time spent foraging (energy maximisers) [14]. In birds of prey the perch hunting (sit-and-wait) strategy is expected to be applied by energy maximisers whereas active hunting is expected to be used by time minimizers [8]. These two strategies rather reflect the extremes of foraging behaviour, which is more likely to be a continuum between the two extremes [8,15]. How long and how actively birds need to forage to meet their energetical needs also depends on environmental conditions and individual factors, meaning that one strategy or another may be more advantageous under certain conditions [8,15,16]. Indeed, meteorological factors, habitat composition and food availability can influence foraging behaviour and consequently also activity patterns [1,17].

Challenging meteorological conditions, including low temperatures, high precipitation, and high wind speeds, have the potential to affect the behaviour of birds of prey in multiple ways. For instance, low temperatures, strong winds and wet plumage increase the amount of energy required for thermoregulation and movement [17–20] and as a result birds may benefit from reducing activity and seeking sheltered roosts during such conditions [2,17,21]. In addition, rain and wind generate noise and movement in the vegetation cover, masking the movement of potential prey [22,23] and reducing hunting success [24,25]. As a result of increased energetic costs combined with reduced hunting success, birds of prey decrease their hunting activity during such challenging periods [24–29].

Besides meteorological factors relative energetic costs of hunting may also depend on the interplay between habitat and prey availability. Hunting suitable prey in favourable habitat may decrease the time and movement intensity animals need to invest to hunt, decreasing energy allocated to foraging [5,6]. Individual differences in habitat and/or prey preference may result in different activity or movement patterns when exposed to the same environmental conditions [30,31]. Barn owls shows colour-morph specific differences in habitat use and prey species choice. Reddish-brown individuals tend to prey on voles and prefer open habitats, while whitish owls prefer murids and complex habitats including wooden structures [32–35], where murids are particularly abundant after harvest and during winter [36–38].

In the present study we used GPS and accelerometer data from tagged western barn owls (*Tyto alba*), a species which inhabits agriculturally dominated areas and shows high breeding site fidelity, even during the non-breeding period [39,40]. The main aim is to understand the activity pattern of barn owls during a period, when mortality can be exceptionally high [41] and temperatures are below the thermoneutral zone of barn owls [42], resulting in increased energy requirements for thermoregulation. Since recent studies have shown that barn owl habitat selection changes between the breeding and non-breeding periods [39,43], as a function of prey availability [39], we are now investigating the activity patterns derived from accelerometer data and the associated energetic consequences [44,45] for foraging under different environmental conditions. To do so, we 1) explored the activity pattern of barn owls during the non-breeding period on a nightly and a seasonal basis. 2) analysed how barn owl activity patterns are related to weather conditions and how barn owl activity patterns are related to prey availability within different habitats.

In our initial analysis of activity patterns during the non-breeding period, we predict 1 a) observing variations in activity levels throughout the night: We hypothesize that owls will allocate their energy towards hunting during a specific, potentially most productive period at night. We also expect 1b) activity patterns to change as the beginning of the breeding season approaches. We further expect 1c) that this predicted change will be sex-specific, as the two sexes have different reproductive roles and investments. For analysis 2) we expect that 2a) barn owls will reduce their activity during nights with unfavourable weather conditions such as low temperatures, rain, or increased wind speeds [24,25,27–29]. The strongest effect is expected to occur during rain, as rain partially impedes movement [29], reduces plumage insulation [19] and affects the audibility of prey [28]. 2b) based on the described differences in habitat and prey preferences we expect owls to respond differently to prey availability within certain habitat types, according to their sex [46] and plumage coloration [32,33,35].

Material and Methods

Study area and study population

Our research focused on a population of barn owls located in western Switzerland (46°49'N, 06°56'E). This population inhabits an area of approximately 1,000 km^2 dominated by intensive agriculture, interspersed with villages and forests. The area can be divided into four distinct geographical regions which slightly differ in topography and land use: the plain of Orbe, the plain of the Broye, Haut-Fribourg, and Gros de Vaud. In our study area, barn owls almost exclusively breed in the more than 400 nest boxes that have been installed in rural buildings. In this central European region, the main prey for barn owls includes voles (*Arvicola sp.*, *Microtus sp.*) and murids (*Apodemus sp.*) [47,48]. The breeding season for barn owls in this area is from February to September [49] and is followed by a resident wintering period.

Individual owl data and tag deployment

Adult owls were captured at their nest site when their offspring were 25 to 35 days old, by using a sliding door trap triggered by the adult bird entering the nest box. Owls received a multisensory tag containing a GPS, a tri-axial acceleration sensor (Axy Trek, TechnoSmart, Italy) combined with a VHF sender (µTag ,Swiss Ornithological Institute, Switzerland), attached as a wing loop harness using spectra-tubular filament (4.7 mm, polyethylene, Bally Ribbon Mills, US). The tag including harness weighed <13 g (which is <5% of body mass, mean body mass of birds before tagging: 297 g, range: 260-440 g, lower limit for equipment: 260g). GPS were programmed to fix one position per hour for two half-nights each week (7-12 pm and 0-4 am UTC), resulting in an average of 6.6 positions per week. Acceleration was sampled continuously at a frequency of 1 Hz throughout day and night. The VHF transmitters had been scheduled to transmit signals for a week during the upcoming spring, allowing to search for the equipped owls. Of the 164 tags deployed (81 females, 83 males) between 2017 and 2020, 110 tags were recovered (67%), and 66 (35 females, 31 males) contained data collected during winter (November-February). Tags recorded between 6 and 120 days, with a mean of 91 days.

Data on body mass, age, pheomelanin plumage coloration and sex were collected as part of a standardised population monitoring. Sex was identified by the presence (female) or absence (male) of a brood patch. Age of each animal was based on the hatching year or alternatively through estimating the age according to primary and secondary moult patterns; this allows to distinguish between a bird in its second year of life (when there is no moult) or an older bird (which shows moulted feathers) [40]. Pheomelanin-based coloration was estimated in the field by attributing a value between 1 (dark, reddish) and 8 (light, white) to the breast, belly, one flank and the underside of a wing [33]. For each individual, these four values were averaged to obtain one numerical score for pheomelanic plumage coloration. Coloration scored by eye in the field is strongly correlated with spectrometry measures [50].

All manipulations have been performed under the legal authorizations of the department of the consumer and veterinary affairs (VD and FR 2844 and 3213) and the Federal Office of Environment (FOEN).

Acceleration and GPS data

GPS as well as acceleration data were cut to range from calendar week 44 (beginning of November) to the following calendar week 9 (end of February). This duration corresponds to the wintering period without breeding activity [49]. As barn owls are night active, only data recorded during the night was included. Night was defined as the time between sunset and sunrise (sun at 0 degrees on the horizon) at the current date, with a buffer of 1 hour before sunset and after sunrise. Mean length of the nights in our dataset with buffer was 17 hours (range: 14.5 – 17.5 hours).

GPS data were visualized, filtered for duplicated locations and aberrant positions were removed. Depending on the duration of sampling 3 up to 168 locations were registered per animal. Acceleration data were divided in 5 second bins, and summary statistics was calculated for each bin. Dynamic acceleration was calculated for all three axis per bin by subtracting the static acceleration (mean of each of the 3 axes per bin) from the raw acceleration values [51]. Then, using dynamic acceleration, we calculated VeDBA (vectorized dynamic body acceleration) for each bin. VeDBA represents the dynamic components of activity and is correlated with energy expenditure [44,45]. To put this technical term into an ecological context, we will hereafter refer to VeDBA as overall activity. Additionally, the standard deviation of each axis was calculated for each 5 second bin. Using the *clara* clustering algorithm (k-medoids PAM method) from the package “cluster” [52], the dataset was divided into 3 clusters: low, medium, and high activity. Clusters were identified using values of the VeDBA and the standard deviation of the surge and heave axis. The three clusters represent 3 behaviour groups, with the high activity cluster representing active flight, the low activity cluster representing resting, gliding flight, or perching and the cluster with medium activity represents behaviours with intermediate amount of movement like handling prey, preening or a mix of low and high activity behaviours (transition from flying to perching or vice versa). Accuracy of the clustering was assessed by visually inspecting 5% of the data.

Snow cover, wind speed, rainfall, and temperature

Hourly information on temperature, wind speed, rainfall and snow cover were obtained from the weather station of the Swiss meteorological institute (Swissmeteo) located in Payerne, situated in the middle of our study area.

Perch availability

To estimate the number of perches (fence posts, road signs and snow poles) along the different types of roads (minor road, major road, highway, and railway) and along pastures, approximate values were used, determined in the field by random sampling of roads and pastures. The following approximations were used to calculate the number of perches available: There were an average of 0.3 perches per m along highways, 0.06 per m along major roads, 0.03 per m along minor roads, and 0.02 per m along railways. For extensive pastures, which are permanently fenced the whole year round, we estimated 0.018 fence posts per m^2. Additionally, the number of single trees within the landscape was obtained from the TLM3D database of the Swiss federal office of topography (TLM3D, resolution: 0.2-3m, Bundesamt für Landestopografie Swisstopo).

Prey availability (small mammal survey)

We assessed prey availability in the four geographical regions of our study area six times per year, at two-month intervals in four different habitat types: crop rotation (annual crops), grassland (intensive and extensive grassland), border structures (1 m margins along roads), and biodiversity structures (hedges and wildflower areas), using two indirect methods, as described in detail in Bühler et al. [39]. The first method involved counting fresh signs of voles (heaps, holes, and runways of Arvicola sp. and Microtus sp.) along 5 x 1 m transects [53]. The second method involved the placement of plastic plates coated with a thin layer of graphite along each transect for two consecutive nights to evaluate the aboveground activity of all small mammal species [54]. We then counted the number of characteristic small mammal tracks per plate. The number of vole signs and small mammal tracks then served as an index of small mammal presence and activity, hereafter referred to as activity density. In total, nine transects were walked, and nine plates were placed in each habitat type during each counting period. This resulted in a total of 576 transects and the same number of plates for each 2-month period. To obtain continuous estimates of prey availability, two separate generalized additive mixed models (GAMM) were fitted, one for the transect method and one for the track-plate method. Estimates from the first GAMM provide information on vole activity density, hereafter called vole activity density index, and estimates from the second GAMM provide information on total small mammal activity density, hereafter called total small mammal activity density index (for details on the GAMM see Bühler et al. [39]).

Both methods have been shown to correlate well with estimates of relative abundance obtained through live trapping [54,55]. The monitoring conducted in this study reflects the activity density of potential prey and is representative of prey availability, as predators tend to prefer areas with higher prey activity and abundance [56]. Furthermore, previous research has demonstrated synchronous fluctuations in vole populations across large spatial scales in Central Europe [57].

Habitat composition

To be able to calculate prey activity density per habitat type we approximated which habitat was available to the owls at the time the acceleration data was sampled. To do so GPS localisations were grouped weekly and buffered with a 1000 m radius. By buffering the localisations, we accounted for the potential activity radius of the owls (mean distance between successive points: 800 m). Weekly covered areas reached from 3 up to 17 km^2

with a mean area of 6.5 km^2. The areas of different habitat types within these weekly activity areas were then extracted to represent the experienced habitat composition on a weekly basis. For the analysis the following habitat types were extracted: grasslands, crop rotation, border structures (1 m margin between roads, railways, and fields), wildflower areas and hedges. Land use information was collected from cantonal offices (Canton of Vaud: all agricultural land, Canton of Fribourg: permanent perennial crops only) and complemented with habitat mapping in the field. Information on coverage of hedges and border structures was obtained from the TLM3D database of the Swiss federal office of topography (TLM3D, resolution: 0.2-3m, Bundesamt für Landestopografie Swisstopo). When data on coverage of habitats were still missing, information from the previous year was used as a proxy to fill the information gaps (correlation between years: 0.8-1 depending on habitat type).

Statistical analysis

To investigate our first hypothesis and predictions (1a, 1b, 1c), we first described how overall activity changed over the night and over winter. To standardize the length of the nights, we split every night into 100 intervals, with the value 1 corresponding to the beginning of the night minus a buffer of 1 hour (sunset-1h) and value 100 to the end of the night plus a buffer of one hour (sunrise+1h). This procedure allows to analyse the overall nightly activity independent of the length of the nights, which differs throughout the year. To describe the nightly pattern of overall activity, we computed the average VeDBA (Vertical Dynamic Body Acceleration) for each interval throughout all recorded nights per individual. This calculation resulted in 100 data points per individual, representing the progression of overall activity throughout the night. For the seasonal description of overall activity, the mean VeDBA per week for each individual was calculated. We fitted Bayesian generalized additive models including temporal autocorrelation using the function “brm” from the package “brms” [59]. We run one model, including data on both sexes, to describe the nightly activity pattern. Within the model the nightly intervals were specified as smooth term. To analyse the activity patterns over the season we run two separate models one for males and one for females, defining week of the year as smooth term. In all three models a temporal autocorrelation structure was included to account for temporal correlation of the datapoints within each individual. To describe activity changes over time we calculated the first derivative of the fitted model curve [60].

To address our hypothesis regarding weather and prey availability (2a, 2b) we calculated two proxies describing the activity pattern of barn owls. First, as within the previous analysis we used VeDBA as proxy for overall activity by using nightly mean as response variable. Second, the nightly proportion of active flight (number of bins with high activity/total number of bins per night) was calculated, better representing the amount of active displacement. Two separate models were run per sex and response variable (overall activity (VeDBA) and proportion of active flight) again using the function "brm" from the package "brms" [59]. To account for non-linear relationship, squared terms were included whenever appropriate. To address the non-independence among data points and to account for temporal autocorrelation, a random intercept as well as a temporal autocorrelation structure was included for each individual. All explanatory variables where centred and scaled before entering the models. To increase model fit we log-transformed overall activity (VeDBA) and square-root transformed the proportion of active flight.

In our study, we also investigated the relationship between meteorological conditions (2a) and the density of prey activity within different habitat types (2b) in relation to overall activity levels and the proportion of active flight. To accomplish this, we multiplied the prey activity density index (prediction from GAMM) of each habitat type and the percentage of coverage within the weekly activity area of the corresponding habitat type (grassland, crop-rotation, biodiversity structures, border structures). We did this separately using the vole activity density index (resulting values hereafter referred to as vole activity density), and the small mammal activity density index (resulting values hereafter referred to small mammal activity density) within each habitat type.

Meteorological data was included by taking the mean values measured during each night for temperature [°C], wind speed [km/h] and rainfall [mm]. We removed snow cover from our models due to the consistently mild winters observed throughout our study period, with no instances of prolonged and heavy snow cover [61–63]. To explore whether the number of perches affected overall activity and proportion of active flight we included the number of available perches (fence posts, road signs, single trees) per square kilometre in the model set. As animals with bigger weekly activity areas are expected to move more, we included the size of the weekly covered area in both model sets. To assess the hypothesis that nightly overall activity or the proportion of active flight was related to pheomelanin coloration, we incorporated interaction terms involving vole activity density and small mammal activity density. To decrease model complexity interaction terms for which the 95% credible interval (CrI) overlapped with zero were removed from the final model.

The function “brm” of the package “brms” [59] employs Bayesian inference to fit the models. In each model, we ran three chains, each consisting of 20,000 iterations, with a warm-up phase of 5,000 iterations. Default non-informative brms priors were applied to all parameters. We evaluated convergence by utilizing Rhat values (Gelman-Rubin diagnostic) and visually inspecting the Markov chains. We evaluated the model fit by comparing the distribution of the observed outcome variable to simulated datasets generated from the posterior predictive distribution. This assessment was conducted using the "pp_check" function from the "brms" package [59].

All analyses and data treatments were run in R version 4.2.1 [58].

Results

1. Nightly and seasonal patterns

Throughout the night, overall activity showed a distinct pattern. Shortly after sunset, there was an initial increase in overall activity, followed by a slight decrease and finally a plateau. (Figure 1). As the night progressed, there was a gradual increase in overall activity towards the end of the night, followed by a decline towards sunrise.

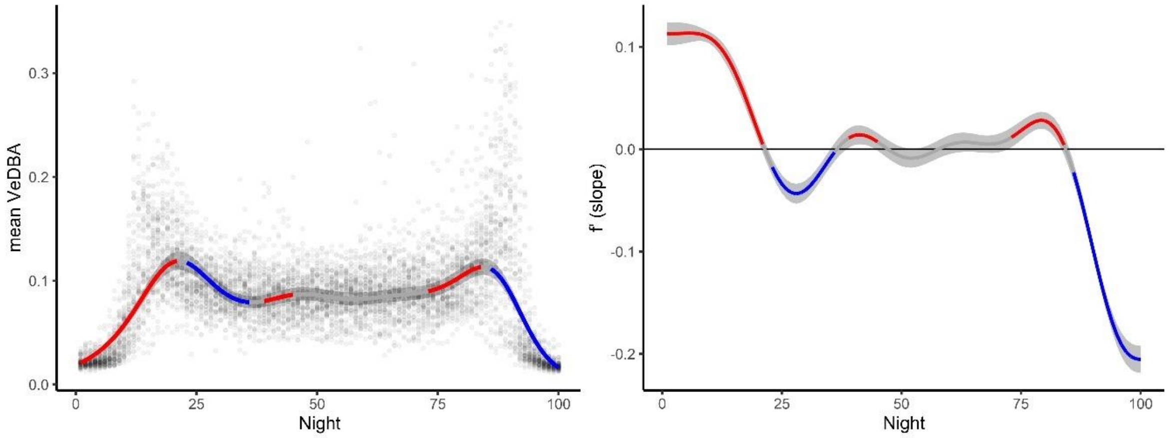


Figure 1: Generalized additive mixed model with 95% CrI (left side panels) and its first derivative (slope) estimation and 95% CrI (right side panels) for 66 individuals. Left panels: Estimated non-linear change of mean VeDBA over the night separated in intervals (1=beginning, 100=end of the night, mean length of night=16.8 hours). Coloured sections indicate rate of change that either increased (red) or decreased (blue) in that specific time frame. Right panels: when the rate of change f' in the y-axis differs from 0, the estimated rate of change is highlighted in blue (decrease) or red (increase).

There was a notable difference in the seasonal pattern between males and females (Figure 2). Males, but not females, showed an increase in overall activity as spring, and the breeding season approached.

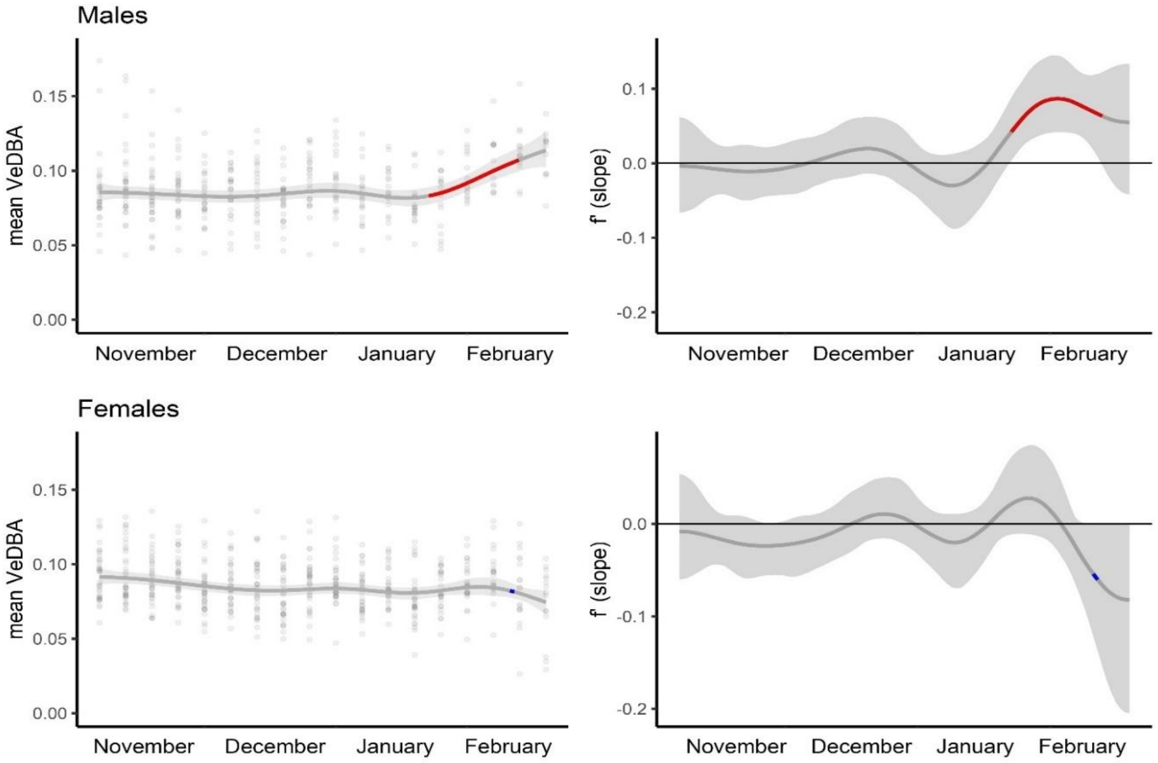


Figure 2: Generalized additive mixed models with 95% CrI (left side panels) and their first derivative (slope) estimations and 95% CrI (right side panels) for 31 males (upper panels) and 35 females (lower panels). Left panels: Estimated non-linear change of mean VeDBA over 18 weeks (calendar week 44 to 9, corresponding to November till February). Coloured sections indicate rate of change that either increased (red) or decreased (blue) in that specific time frame. Right panels: when the rate of change f' in the y-axis differs from 0, the estimated rate of change is highlighted in blue (decrease) or red (increase).

2. Meteorological factors and prey activity density

While rising mean temperature was associated with increasing overall activity, there was no relationship between temperature and proportion of active flight (Table 1, Figure 3). Both mean rainfall and mean wind speed per night showed a non-linear relationship with overall activity and proportion of active flight in both sexes (Table 1, Figure 3). Rainfall was found to be strongly linked with both overall activity and the proportion of active flight. This association resulted in a significant decrease in both overall activity and the proportion of active flight with an increase in the amount of rainfall per night. While both response variables initially showed an increase, they subsequently decreased with higher wind speeds. The size of the weekly activity area was positively related to overall activity and proportion of active flight for both males and females (Table 1).

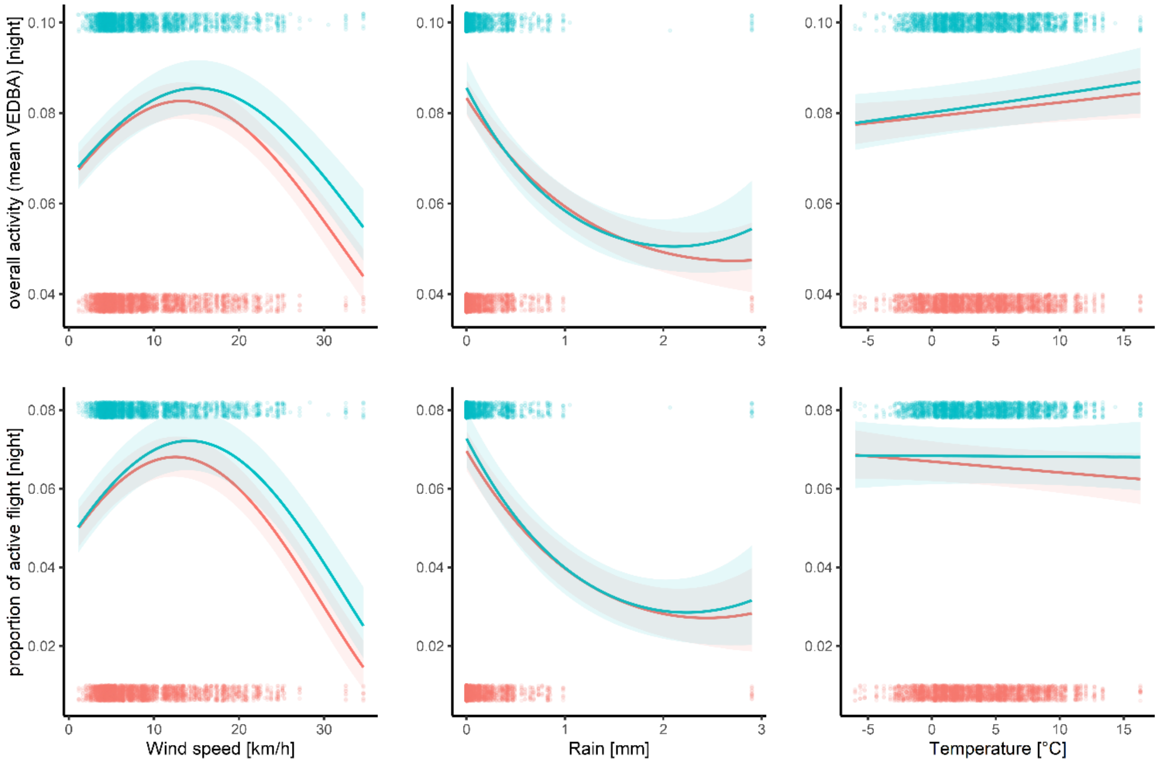


Figure 3: Effect of wind speed (left) and rain (middle) and temperature (right) on female (red) and male (green) overall activity (upper) and proportion of active flight (lower). We present mean estimates of ß and associated 95% credible interval of the posterior distribution of the model in table 1. The models were constructed based on a dataset consisting of 3741 data points for females (35 individuals) and 2810 data points for males (31 individuals).

In females, a decrease in overall activity and proportion of active flight was associated with increasing vole activity density in biodiversity structures, while an increase in overall activity and proportion of active flight was associated with increasing small mammal activity density in grassland and biodiversity structures (Table 1). Further, reddish-brown-coloured females showed an increase in overall activity and the proportion of active flight with increasing small mammal activity density in the crop rotation. In contrast, whitish-coloured females displayed the opposite pattern, with a decrease in overall activity and the proportion of active flight as small mammal activity density in the crop rotation increased (Table1, Figure 4).

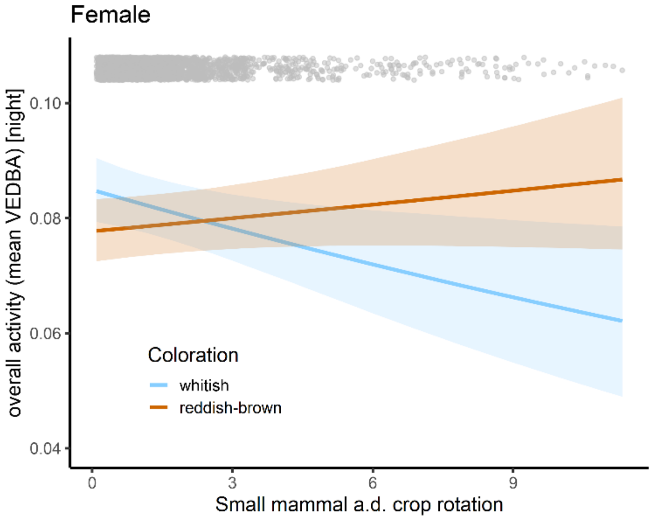


Figure 4: Effect of small mammal activity density in crop rotation in interaction with pheomelanic plumage on nightly mean VeDBA for females. For comprehensive interpretation coloration is presented by 2 values with mean plus standard deviation for whitish and mean minus standard deviation for reddish-brown coloration. We present mean estimates of ß and associated 95% credible interval of the posterior distribution of the model in table 4. The models were constructed based on a dataset consisting of 3741 data points for females (35 individuals) and 2810 data points for males (31 individuals).

In males, an increase in overall activity and the proportion of active flight was observed with increasing vole activity density in border structures. Additionally, overall activity and the proportion of active flight increased with increasing small mammal activity density in crop rotation and decreased as the number of available perches within the landscape increased (Table 1).

Overall activity and the proportion of active flight of reddish-brown, but not whitish, males increased with increasing vole activity density in the crop rotation (Table1, Figure 5).

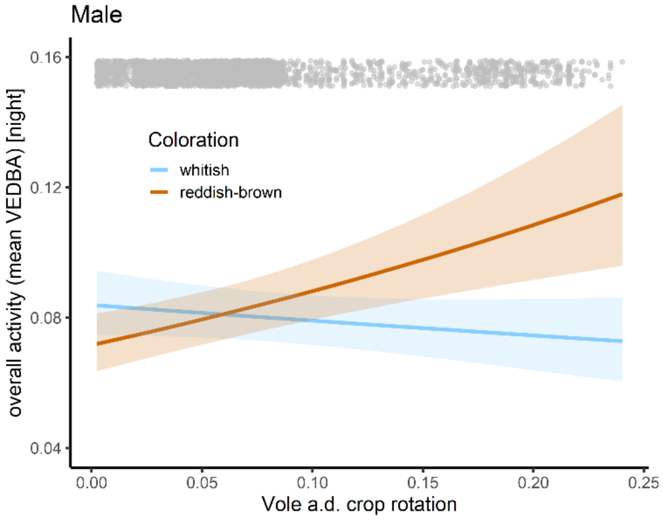


Figure 5: Effect of vole activity density in crop rotation in interaction with pheomelanic plumage coloration on nightly mean VeDBA for males. For comprehensive interpretation coloration is presented by 2 values with mean plus standard deviation for whitish and mean minus standard deviation for reddish-brown coloration. We present mean estimates of ß and associated 95% credible interval of the posterior distribution of the model in table 4. The models were constructed based on a dataset consisting of 3741 data points for females (35 individuals) and 2810 data points for males (31 individuals).

Table 1: Mean effect sizes with 95% Bayesian credible interval (CrI) for the linear-mixed effect models with nightly overall activity (left, log transformed) and proportion of active flight (right, square-root transformed) as a response variable. Coloration, prey activity density per habitat type and its interactions as well as meteorological factors, the total activity area and the amount of perches available were introduced as explanatory variables and individual as random intercept. The models were constructed based on a dataset consisting of 3741 data points for females (35 individuals) and 2810 data points for males (31 individuals). Effects which CrI exclude zero are shown in bold. Dashes in the fixed effects columns indicate interaction terms that were excluded from the final model because their 95% CrI included 0.

	Overall activity (mean VEDBA) [log] ß mean (95% CrI)		Active flight [sqr] ß mean (95% CrI)	
	female	male	female	male
Intercept	**-2.521** **(-2.568 to -2.475)**	**-2.505** **(-2.572 to -2.438)**	**0.257** **(0.247 to 0.266)**	**0.261** **(0.248 to 0.275)**
Coloration	0.021 (-0.022 to 0.065)	-0.015 (-0.086 to 0.054)	0.004 (-0.005 to 0.012)	-0.005 (-0.019 to 0.009)
Mean temperature [°C]	**0.014** **(0.001 to 0.028)**	**0.019** **(0.003 to 0.034)**	-0.002 (-0.005 to 0.001)	0.000 (-0.003 to 0.003)
Mean wind speed [km/h]	**0.071** **(0.053 to 0.088)**	**0.084** **(0.063 to 0.104)**	**0.012** **(0.009 to 0.016)**	**0.016** **(0.012 to 0.02)**
(Mean wind speed [km/h])^2	**-0.045** **(-0.053 to -0.037)**	**-0.038** **(-0.046 to -0.029)**	**-0.009** **(-0.011 to -0.008)**	**-0.008** **(-0.010 to -0.007)**
Mean rainfall [mm]	**-0.100** **(-0.119 to -0.080)**	**-0.119** **(-0.141 to -0.096)**	**-0.019** **(-0.023 to -0.016)**	**-0.021** **(-0.026 to -0.017)**
(Mean rainfall [mm])^2	**0.005** **(0.002 to 0.007)**	**0.007** **(0.005 to 0.010)**	**0.001** **(0.001 to 0.001)**	**0.001** **(0.001 to 0.002)**
Vole activity density grassland	0.011 (-0.013 to 0.035)	0.015 (-0.019 to 0.048)	0.004 (-0.001 to 0.009)	0.003 (-0.004 to 0.009)
Vole activity density crop rotation	0.004 (-0.023 to 0.030)	0.040 (-0.001 to 0.081)	0.002 (-0.004 to 0.007)	**0.012** **(0.003 to 0.020)**
Vole activity density border structures	-0.027 (-0.055 to 0.001)	**0.040** **(0.004 to 0.076)**	-0.004 (-0.010 to 0.002)	**0.010** **(0.003 to 0.017)**
Vole activity density biodiv. structures	**-0.053** **(-0.078 to -0.027)**	0.025 (-0.016 to 0.069)	**-0.009** **(-0.014 to -0.004)**	0.005 (-0.003 to 0.014)
Small mammal activity density grassland	**0.038** **(0.018 to 0.059)**	0.016 (-0.010 to 0.042)	**0.008** **(0.004 to 0.012)**	0.003 (-0.002 to 0.009)
Small mammal activity density crop rotation	-0.013 (-0.033 to 0.006)	**0.068** **(0.045 to 0.091)**	-0.002 (-0.006 to 0.002)	**0.013** **(0.009 to 0.018)**
Small mammal activity density border structures	-0.005 (-0.023 to 0.013)	0.023 (-0.008 to 0.053)	0.001 (-0.003 to 0.005)	0.005 (-0.001 to 0.011)
Small mammal activity density biodiv. structures	**0.041** **(0.017 to 0.065)**	-0.019 (-0.047 to 0.010)	**0.006** **(0.001 to 0.011)**	-0.005 (-0.011 to 0.001)
Weekly activity area [km^2]	**0.056** **(0.039 to 0.072)**	**0.059** **(0.038 to 0.080)**	**0.013** **(0.009 to 0.016)**	**0.014** **(0.009 to 0.018)**
Number of perches/km^2	-0.015 (-0.048 to 0.018)	**-0.074** **(-0.125 to -0.022)**	-0.006 (-0.013 to 0.001)	**-0.017** **(-0.027 to -0.006)**
Coloration: Small mammal activity density crop rotation	**-0.027** **(-0.046 to -0.008)**	---	**-0.005** **(-0.009 to -0.001)**	**---**
Coloration: Vole activity density crop rotation	**---**	**-0.073** **(-0.11 to -0.037)**	---	**-0.015** **(-0.022 to -0.007)**
Random effects	Variance (95% CrI)			
Individual random effect	0.130 (0.098 to 0.173)	0.177 (0.126 to 0.248)	0.026 (0.020 to 0.035)	0.036 (0.025 to 0.050)

Discussion

Our study is among the rare ones investigating activity patterns outside the breeding period and potentially the first to do so for nocturnal birds of prey. Overall activity, measured as VeDBA, which has been shown to correlate with energy expenditure [44,45], serves as an indicator of the amount of energy expended by an individual under specific environmental conditions. Here we have shown that barn owls have a distinct pattern of overall activity during the night, with two peaks of activity. Additionally, male activity changed as the breeding period approaches. Overall activity and the proportion of active flight were directly related to weather conditions and prey availability. Understanding these relationships is important because, due to the increased energy cost of thermoregulation during the non-breeding season [1,2], the energy expended on activity may have a direct impact on individual fitness. Furthermore, individual- and especially sex-specific reactions towards changes in food availability may directly act on species demography as selection may act stronger on a certain group of individuals.

Nightly and seasonal activity pattern

The nightly activity patterns of barn owls displayed two distinct peaks, one at the start of the night and another at the end, with a period of relatively stable activity during the middle of the night. These two peaks coincide with nocturnal peaks in prey activity [64–66], suggesting that increased owl activity corresponds to increased hunting effort at times when hunting is likely to be most profitable.

Predator activity is typically closely linked to prey behaviour [67–69]. In response, prey species adapt their activity patterns to avoid periods of increased predation risk [70,71]. The extent to which prey should modify their behaviour in response to predators depends on the level of predatory pressure and the associated trade-offs between the benefits and costs of predator avoidance [70,72]. For example, prey species may make trade-offs between predation risk and thermoregulatory advantages [73]. During winter, small mammals benefit energetically from shifting their activity patterns towards daytime to reduce thermoregulatory costs [64]. Common voles change from predominantly nocturnal to diurnal activity during winter [65]. Wood mice however display a shift from unimodal to bimodal activity patterns, with increased activity after dawn and before sunrise [66]. Given that more active prey offers a greater opportunity for successful hunting, barn owls are believed to adjust their hunting activity to coincide with the periods when prey activity is at its peak [56,74]. Owls may therefore follow a "time minimizer" strategy, concentrating the majority of their activity towards short time periods around dusk and dawn when prey is most active and accessible [8,14]. Outside of these peak periods overall activity may remain low, indicating that owls do not completely cease activity but reduce the intensity. This strategy may enable them to conserve energy while still being able to take advantage of a hunting opportunity when it presents itself.

The seasonal activity pattern shows a clear increase in activity for males towards the end of January, but not for females. This divergence between males and females is likely due to their different reproductive roles. Towards the end of winter males start exploring and occupying nest sites along with initiating courtship behaviour [40,75]. Searching for suitable breeding sites and defend it against competitors, may result in increased activity levels. Furthermore, male barn owls deposit prey in the nest box as a part of their courtship behaviour [40,75], which requires increased hunting effort and thus activity.

Meteorological conditions

Weather conditions influenced the behaviour of barn owls, both in terms of overall activity and the proportion of active flight. Specifically, colder temperatures, strong winds, and rain were linked to decreased levels of overall activity and/or proportion of active flight in barn owls.

Temperatures above and below the thermoneutral zone of animals result in increased energetic costs and animals react by reducing activity during thermally challenging periods [76–78]. During the study period, temperatures in our research area ranged from -6 - 16 °C throughout the non-breeding season. This range falls below the barn owl's thermoneutral zone, which is between 23-35°C [42]. Consequently, when temperatures fall below their thermoneutral zone during the non-breeding season, barn owls expend more energy even when at rest than during the warmer breeding season. Hence, it may become crucial for owls to minimize their activity during cold nights to conserve energy [77]. Our study showed that while overall nightly activity decreased with decreasing temperature, the proportion of active flight remained relatively constant. This suggests that the proportion of active flight, despite its higher energy demands, may have a minimum threshold beyond which it cannot be further reduced. Consequently, barn owls may have the ability to reduce different forms of movement but may need to keep the proportion of active flight relatively stable. Alternatively, it is possible that barn owls adjust their flight speed during colder nights to conserve energy. This is because overall activity tends to increase with flight intensity and speed [79], which could also explain the observed pattern of maintaining a constant amount of active flight while showing lower overall activity during colder periods.

During rainy nights, both active flight and mean overall activity decreased for both male and female owls. Rain has strong effects on hunting success and flight performance. Firstly, rain creates noise and movement in the vegetation, which impairs the ability of birds of prey to detect their prey acoustically and visually [28], even though potential prey, such as small mammals, may be more active [23]. Secondly, flying with wet feathers is more energy consuming [29], and reduces insulation efficiency [19]. To avoid disproportionately high energy expenditure in unfavourable weather conditions, owls minimize activity and prioritize roosting to conserve energy [2], as has been demonstrated in other bird of prey species [26–29].

The response of owls to wind is only partially consistent with our hypothesis, as we expected a constant decrease in activity with increasing wind speed. Instead, both sexes showed an initial increase in overall activity and active flight proportion up to wind speeds of 15 km/h, followed by a decrease at higher wind speeds. Light winds can positively affect the hunting efficiency of birds by increasing commuting flight speeds in tailwinds and flight control in headwinds [80,81]. However, when wind speeds exceed a certain threshold, energy expenditure for movement and thermoregulation increases dramatically [20,21,82]. Stronger winds can hamper the hunting success of birds of prey by causing noise and movement in the surrounding vegetation, making it more difficult for birds to locate their prey [24,25,83,84]. As a result, owls may undergo a behavioural shift and switch from hunting to roosting.

Prey availability

Landscape composition and habitat features, among other environmental factors, can influence animal behaviour such as hunting strategies and the resulting energy expenditure [76,85]. Habitat type plays a crucial role in shaping predator-prey interactions, as it can lead to variation in prey species, prey density, and prey accessibility across different habitat types [86]. In order to optimize their hunting efficiency and to conserve energy, predators often adapt their hunting behaviour based on factors such as the specific prey species, prey availability, and the characteristics of the prey's habitat [5, 6, 87].

Our findings indicate that barn owls adapt their hunting behaviour based on the availability of prey species within specific habitat types. In open habitats, such as grassland and crop rotation, with limited perching opportunities we observed an increase in overall activity and the proportion of active flight as prey activity increased. This suggests that owls intensify their hunting efforts when prey is abundant in these environments. Conversely, in areas with more perching opportunities, both overall activity and the proportion of active flight decreased. For male barn owls, we further observed a negative correlation between the of number of perches and both overall activity and proportion of active flight.

Our results also indicate that females adapt their hunting strategy based on the behaviour of the most prevalent prey species. Biodiversity structures, such as hedgerows and wildflower patches, contain a high diversity and density of small mammal species [39,88–91]. When more stealthy prey, such as voles, are present in biodiversity structures, overall activity and the proportion of active flight decreases in females, indicating a switch to perch hunting. Common voles, one of the main prey species of barn owls [47], are primarily dwelling underground, occupying small territories [92] and cold temperatures and reduced vegetation cover reduce their activity [65,93], potentially making the pursuit of this prey time intensive. Adopting a sit-and-wait hunting technique in habitats where vole activity is high and perching opportunities are manyfold, could lead to significant energy advantages. Such a shift towards perch hunting has been observed in birds of prey during the colder, energy-demanding non-breeding period [10–12] and might be particularly important for females, as their higher body mass makes flying more energetically costly [94]. The rise in both, overall activity and active flight, in relation to an increase in small mammal activity density within biodiversity structures but also grasslands suggest a potential link between the agility and mobility of prey and the effectiveness of active flight hunting. Males displayed a similar pattern when small mammal activity density was high in crop-rotation. Plenty of active prey may increase the success of aerial hunting, making this more energy-intensive hunting strategy advantageous. Nevertheless, such a more energetically demanding hunting approach may only be beneficial when prey density exceeds a certain threshold [6]. Under scenarios where small mammal activity density is low and hunting success diminishes, owls might profit from transitioning to an energy-efficient sit-and-wait hunting strategy.

Females differing in pheomelanic plumage coloration also showed different responses to higher small mammal activity density. While reddish-brown females showed a slight increase in overall activity and proportion of active flight with increasing activity density of small mammals in crop rotation, whitish individuals displayed the opposite pattern. During the breeding period the preferred prey of whitish individuals within our study area are rather active and above ground moving murids [32]. If such active and above ground moving prey are available in crop rotation fields, which cover a big part of the agriculturally manged landscape and are usually low in vegetation cover during winter, they may also be of high accessibility for barn owls. Being specialised in hunting agile prey moving above ground, whitish females may be able to reduce their foraging time compared to their reddish-brown coloured counterparts. Moonlit nights may provide an interesting scenario, where whitish coloured females might exhibit enhanced hunting efficiency within an open habitat. The reflection of the moonlight on the white body parts of the owls can lead to a "freeze effect" in their prey, making it easier for them to catch rather active targets [95].

Reddish-brown coloured males, which show a preference to hunt voles [32,33,35] showed an increase in overall activity and proportion of active flight with increasing vole activity density in crop rotation. If crop rotation field have a high vole population, voles may be accessible within the short-vegetated crop rotation fields, but these fields are rather large and do not provide many perching opportunities. As previously mentioned for females, when hunting more cryptic prey like voles, perch hunting may be the most energy-efficient strategy. Hunting voles in perch-deprived crop rotation fields may require an increased duration of active flight during hunting, leading to higher overall activity and a greater reliance on active flight. This strategy may be predominantly used by reddish-brown male barn owls and become more common when vole activity density is high in rather open habitats. Hence, it is plausible that owls may benefit from a specific type of prey in a particular habitat, but only when this combination enables them to employ the most efficient hunting strategy.

Overall, these results indicate that barn owls may follow different hunting strategies depending on prey and habitat type. To switch from an energy saving hunting strategy to a more active behaviour might be beneficial and owls may actively decide to switch behaviour to maximise energy intake. Yet, if a habitat-adapted hunting strategy is not possible because prey density is too low, owls may be forced to use a more energy-intensive hunting method. Such a shift could potentially jeopardize the equilibrium between their energy intake and expenditure. A higher resolution of accelerometer data would allow to calculate successful hunting attempts allowing to disentangle hunting flights from successful hunting strikes. Such data would also allow a more detailed view on how owls exploit different habitat types and if hunting behaviour differs in relation to habitat types and perch availability depending on hunting success.

Conclusions

Barn owls appear to adjust their peak activity to coincide with the activity patterns of their prey, which are primarily active at the beginning and end of the night. Moreover, during the spring season, we observed a notable increase in male activity, likely attributed to behaviours associated with breeding.

In our previous study [39], we established that barn owls prefer prey-rich habitat types during winter. Building upon that, our current research demonstrates that prey activity density within certain habitats is linked with overall activity and proportion of active flight. Our research indicates that depending on prey activity density barn owls seem to choose different hunting strategies. Furthermore, within each sex, the response to prey activity density appears to be also linked to individual prey species preference.

Our study suggests that variations in activity patterns may stem from differences in sex and colour-specific habitat and prey preferences. However, to delve deeper into the intricate interplay between habitat, prey availability, plumage coloration, and sex, more detailed and fine-scaled data is required. Such future investigations would help to shed further light on the complex dynamics influencing activity patterns and the resulting energy expenditure in barn owls.

Outlook

For final publication of this chapter, we will further investigate the role of sex and plumage coloration on movement energetics. We aim to re-analyse our accelerometer data using an approach (e.g. proposed by [96]) which enables to annotate different behaviours to our accelerometer patterns. During our study period we furthermore recaptured 11 individuals which were equipped with tags programmed to register fine scaled data over shorter period (1 localisation/10sec and 25 Hz acceleration data). These fine scale data could help to further investigate differences in movement energetics in relation to sex and plumage coloration. Given the results of San-Jose et al. [95] showing that differently coloured barn owls profited differently from moon illuminated nights we also aim to include moonlight illumination in our analysis. Furthermore, we aim to make the link between activity related energy expenditure during the non-breeding period and survival and reproduction. For example, by analysing if activity is related to onset of reproduction or reproductive success.

References

1. Biebach H. 1996 Energetics of Winter and Migratory Fattening. In *Avian Energetics and Nutritional Ecology*, pp. 280–323. Springer, Boston, MA. (doi:10.1007/978-1-4613-0425-8_9)
2. McCafferty DJ, Moncrieff JB, Taylor IR. 2001 How much energy do barn owls (*Tyto alba*) save by roosting? *J Therm Biol* **26**, 193–203. (doi:10.1016/S0306-4565(00)00042-5)
3. Norrdahl K, Klemola T, Korpimäki E. 2002 Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos* **99**, 419–430. (doi:10.1034/J.1600-0706.2002.12025.X)
4. Marra P, Cohen E, Loss S, Rutter J, Tonra C. 2015 A call for full annual cycle research in animal ecology. *Biol Lett* **11**. (doi:10.1098/rsbl.2015.0552)
5. MacArthur RH, Pianka ER. 1966 On Optimal Use of a Patchy Environment. *Am Nat* **100**, 603–609. (doi:10.1086/282454)
6. Pyke GH, Pulliam HR, Charnov EL. 1977 Optimal Foraging. *Q Rev Biol* **52**, 137–154. (doi:10.1086/409852)
7. Kowalczyk ND, Chiaradia A, Preston TJ, Reina RD. 2015 Fine-scale dietary changes between the breeding and non-breeding diet of a resident seabird. *R Soc Open Sci* **2**. (doi:10.1098/RSOS.140291)
8. Nadjafzadeh M, Hofer H, Krone O. 2016 Sit-and-wait for large prey: Foraging strategy and prey choice of White-tailed Eagles. *J Ornithol* **157**, 165–178. (doi:10.1007/s10336-015-1264-8)
9. Beeston R, Baines D, Richardson M. 2005 Seasonal and between-sex differences in the diet of Black Grouse *Tetrao tetrix*. *Bird Study* **52**, 276–281. (doi:10.1080/00063650509461400)
10. Masman D, Daan S, Dijkstra C. 1988 Time Allocation in the Kestrel (Falco tinnunculus), and the Principle of Energy Minimization. *J Anim Ecol* **57**, 411. (doi:10.2307/4914)
11. Pettifor RA. 1983 Seasonal variation, and associated energetic implications, in the hunting behaviour of the Kestrel. *Bird Study* **30**, 201–206. (doi:10.1080/00063658309476797)
12. Meunier FD, Verheyden C, Jouventin P. 2000 Use of roadsides by diurnal raptors in agricultural landscapes. *Biol Conserv* **92**, 291–298. (doi:10.1016/S0006-3207(99)00094-4)
13. Grémillet D, Wanless S, Carss DN, Linton D, Harris MP, Speakman JR, Maho Y Le. 2001 Foraging energetics of arctic cormorants and the evolution of diving birds. *Ecol Lett* **4**, 180–184. (doi:10.1046/J.1461-0248.2001.00214.X)
14. Schoener TW. 1971 Theory of Feeding Strategies. *Annu Rev Ecol Syst* **2**, 369–404. (doi:10.1146/ANNUREV.ES.02.110171.002101)
15. Cecere JG, De Pascalis F, Imperio S, Ménard D, Catoni C, Griggio M, Rubolini D. 2020 Inter-individual differences in foraging tactics of a colonial raptor: Consistency,

weather effects, and fitness correlates. *Mov Ecol* **8**, 1–13. (doi:10.1186/S40462-020-00206-W)

16. Pyke GH. 1984 Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics* **15**, 523–575. (doi:10.1146/ANNUREV.ES.15.110184.002515)
17. Stalmaster M V., Gessaman JA. 1984 Ecological Energetics and Foraging Behavior of Overwintering Bald Eagles. *Ecol Monogr* **54**, 407–428. (doi:10.2307/1942594)
18. Hamilton KL. 1985 Food and energy requirements of captive barn owls *Tyto alba*. *Comp Biochem Physiol A Physiol* **80**, 355–358. (doi:10.1016/0300-9629(85)90050-7)
19. Kennedy RJ. 1970 Direct effects of rain on birds: a review. *British Birds* **63**.
20. Carr JM, Lima SL. 2012 Heat-conserving postures hinder escape: a thermoregulation–predation trade-off in wintering birds. *Behavioral Ecology* **23**, 434–441. (doi:10.1093/BEHECO/ARR208)
21. Walsberg GE. 1986 Thermal Consequences of Roost-site Selection: The Relative Importance of Three Modes of Heat Conservation. *Auk* **103**, 1–7. (doi:10.1093/AUK/103.1.1)
22. Vickery WL, Bider JR. 1981 The Influence of Weather on Rodent Activity. *J Mammal* **62**, 140–145. (doi:10.2307/1380484)
23. Wróbel A, Bogdziewicz M. 2015 It is raining mice and voles: which weather conditions influence the activity of *Apodemus flavicollis* and *Myodes glareolus*? *Eur J Wildl Res* **61**, 475–478. (doi:10.1007/S10344-014-0892-2)
24. Van Manen W. 2001 Influence of weather circumstances on behaviour and hunting success of wintering long-eared owls Asio otus. *Limosa* **74**, 81–86.
25. Kämpfer S, Engel E, Fartmann T. 2022 Weather conditions determine reproductive success of a ground-nesting bird of prey in natural dune grasslands. *J Ornithol* **163**, 855–865. (doi:10.1007/s10336-022-01999-w)
26. Newton I. 1978 Feeding and development of Sparrowhawk *Accipiter nisus* nestlings. *J Zool* **184**, 465–487. (doi:10.1111/J.1469-7998.1978.TB03302.X)
27. Sergio F. 2003 From individual behaviour to population pattern: weather-dependent foraging and breeding performance in black kites. *Anim Behav* **66**, 1109–1117. (doi:10.1006/ANBE.2003.2303)
28. Lehikoinen A, Byholm P, Ranta E, Saurola P, Valkama J, Korpimäki E, Pietiäinen H, Henttonen H. 2009 Reproduction of the common buzzard at its northern range margin under climatic change. *Oikos* **118**, 829–836. (doi:10.1111/J.1600-0706.2008.17440.X)
29. Olsen P, Olsen J. 1992 Does Rain Hamper Hunting by Breeding Raptors? *Emu - Austral Ornithology* **92**, 184–187. (doi:10.1071/MU9920184)
30. Hertel AG, Efrat R, Reznikov K, Sapir N, Berger-Tal O, Mueller T. 2023 Time constraints may pace the ontogeny of movement behaviour. *Proceedings of the Royal Society B* **290**. (doi:10.1098/RSPB.2022.2429)

31. Hertel AG, Royauté R, Zedrosser A, Mueller T. 2021 Biologging reveals individual variation in behavioural predictability in the wild. *Journal of Animal Ecology* **90**, 723–737. (doi:10.1111/1365-2656.13406)

32. Roulin A. 2004 Covariation between plumage colour polymorphism and diet in the Barn Owl. *Ibis* **146**, 509–517. (doi:10.1111/j.1474-919x.2004.00292.x)

33. Dreiss AN, Antoniazza S, Burri R, Fumagalli L, Sonnay C, Frey C, Goudet J, Roulin A. 2012 Local adaptation and matching habitat choice in female barn owls with respect to melanic coloration. *J Evol Biol* **25**, 103–114. (doi:10.1111/j.1420-9101.2011.02407.x)

34. Charter M, Leshem Y, Izhaki I, Roulin A. 2015 Pheomelanin-based colouration is correlated with indices of flying strategies in the Barn Owl. *J Ornithol* **156**, 309–312. (doi:10.1007/S10336-014-1129-6)

35. Charter M, Peleg O, Leshem Y, Roulin A. 2012 Similar patterns of local barn owl adaptation in the Middle East and Europe with respect to melanic coloration. *Biological Journal of the Linnean Society* **106**, 447–454. (doi:10.1111/j.1095-8312.2012.01863.x)

36. Todd IA, Tew TE, Macdonald DW. 2000 Arable habitat use by wood mice (*Apodemus sylvaticus*). 1. Macrohabitat. *J Zool* **250**, 299–303. (doi:10.1111/j.1469-7998.2000.tb00773.x)

37. Tattersall FH, Macdonald DW, Hart BJ, Manley WJ, Feber RE. 2001 Habitat use by wood mice (*Apodemus sylvaticus*) in a changeable arable landscape. *J Zool* **255**, 487–494. (doi:10.1017/S095283690100156X)

38. Heroldová M, Bryja J, Zejda J, Tkadlec E. 2007 Structure and diversity of small mammal communities in agriculture landscape. *Agric Ecosyst Environ* **120**, 206–210. (doi:10.1016/j.agee.2006.09.007)

39. Bühler R, Schalcher K, Séchaud R, Roulin A, Almasi B. 2023 Influence of prey availability on habitat selection during the non-breeding period in a resident bird of prey. *Mov Ecol* **11**. (doi:10.1186/s40462-023-00376-3)

40. Taylor IR. 1994 *Barn owls*. 1st edn. Cambridge: Cambridge University Press.

41. Altwegg R, Roulin A, Kestenholz M, Jenni L. 2006 Demographic effects of extreme winter weather in the barn owl. *Oecologia* **149**, 44–51. (doi:10.1007/s00442-006-0430-3)

42. McCafferty DJ, Moncrieff JB, Taylor IR, Boddie GF. 1998 The use of IR thermography to measure the radiative temperature and heat loss of a barn owl (*Tyto alba*). *J Therm Biol* **23**, 311–318. (doi:10.1016/S0306-4565(98)00022-9)

43. Séchaud R, Schalcher K, Machado AP, Almasi B, Massa C, Safi K, Roulin A. 2021 Behaviour-specific habitat selection patterns of breeding barn owls. *Mov Ecol* **9**, 1–11. (doi:10.1186/s40462-021-00258-6)

44. Elliott KH, Le Vaillant M, Kato A, Speakman JR, Ropert-Coudert Y. 2013 Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biol Lett* **9**. (doi:10.1098/RSBL.2012.0919)

45. Qasem L, Cardew A, Wilson A, Griffiths I, Halsey LG, Shepard ELC, Gleiss AC, Wilson R. 2012 Tri-axial dynamic acceleration as a proxy for animal energy expenditure;

should we be summing values or calculating the vector? *PLoS One* **7**, e31187. (doi:10.1371/journal.pone.0031187)

46. Pande S, Dahanukar N. 2012 Reversed Sexual Dimorphism and Differential Prey Delivery in Barn Owls (*Tyto alba*). *Journal of Raptor Research* **46**, 184–189. (doi:10.3356/JRR-10-09.1)
47. Roulin A. 2004 The function of food stores in bird nests: Observations and experiments in the Barn Owl *Tyto alba*. *Ardea* **92**, 69–78.
48. Frey C, Sonnay C, Dreiss A, Roulin A. 2010 Habitat, breeding performance, diet and individual age in Swiss Barn Owls (*Tyto alba*). *J Ornithol* **152**, 279–290. (doi:10.1007/s10336-010-0579-8)
49. Béziers P, Roulin A. 2016 Double brooding and offspring desertion in the barn owl Tyto alba. *J Avian Biol* **47**, 235–244. (doi:10.1111/jav.00800)
50. Dreiss AN, Roulin A. 2010 Age-related change in melanin-based coloration of Barn owls (*Tyto alba*): females that become more female-like and males that become more male-like perform better. *Biological Journal of the Linnean Society* **101**, 689–704. (doi:10.1111/J.1095-8312.2010.01503.X)
51. Gleiss AC, Wilson RP, Shepard ELC. 2011 Making overall dynamic body acceleration work. *Methods Ecol Evol* **2**, 23–33. (doi:10.1111/j.2041-210X.2010.00057.x)
52. Maechler M *et al.* 2022 cluster: ‘Finding Groups in Data’.
53. Apolloni N, Grüebler MU, Arlettaz R, Gottschalk TK, Naef-Daenzer B. 2017 Habitat selection and range use of little owls in relation to habitat patterns at three spatial scales. *Anim Conserv* **65**, 210. (doi:10.1111/acv.12361)
54. Glennon MJ, Porter WF, Demers CL. 2002 An alternative field technique for estimating diversity of small-mammal populations. *J Mammal* **83**, 734–742. (doi:10.1644/1545-1542(2002)083<0734:AAFTFE>2.0.CO;2)
55. Jareño D, Viñuela J, Luque-Larena JJ, Arroyo L, Arroyo B, Mougeot F. 2014 A comparison of methods for estimating common vole (*Microtus arvalis*) abundance in agricultural habitats. *Ecol Indic* **36**, 111–119. (doi:10.1016/J.ECOLIND.2013.07.019)
56. Embar K, Mukherjee S, Kotler BP. 2014 What do predators really want? The role of gerbil energetic state in determining prey choice by Barn Owls. *Ecology* **95**, 280–285. (doi:10.1890/13-0836.1)
57. Fay R, Michler S, Laesser J, Jeanmonod J, Schaub M. 2020 Large-Scale Vole Population Synchrony in Central Europe Revealed by Kestrel Breeding Performance. *Front Ecol Evol* **7**, 512. (doi:10.3389/FEVO.2019.00512)
58. R Development Core Team. 2021 R: A language and environment for statistical computing.
59. Bürkner P-C *et al.* 2023 brms: Bayesian Regression Models using ‘Stan’.
60. Becciu P, Troupin D, Dinevich L, Leshem Y, Sapir N. 2023 Soaring migrants flexibly respond to sea-breeze in a migratory bottleneck: using first derivatives to identify behavioural adjustments over time. *Mov Ecol* **11**, 1–11. (doi:10.1186/S40462-023-00402-4)
61. MeteoSchweiz. 2021 Klimabulletin Winter 2020/21.

62. MeteoSchweiz. 2020 Klimabulletin Winter 2019/20.

63. MeteoSchweiz. 2019 Klimabulletin Winter 2018/19.

64. Guiden PW, Orrock JL. 2020 Seasonal shifts in activity timing reduce heat loss of small mammals during winter. *Anim Behav* **164**, 181–192. (doi:10.1016/J.ANBEHAV.2020.04.014)

65. Hoogenboom I, Daan S, Dallinga JH, Schoenmakers M. 1984 Seasonal change in the daily timing of behaviour of the common vole, *Microtus arvalis*. *Oecologia* **61**, 18–31. (doi:10.1007/BF00379084)

66. Wolton RJ. 1983 The Activity of Free-Ranging Wood Mice *Apodemus sylvaticus*. *J Anim Ecol* **52**, 781. (doi:10.2307/4453)

67. Reynolds P, Gorman ML. 1999 The timing of hunting in short-eared owls (*Asio flammeus*) in relation to the activity patterns of Orkney voles (*Microtus arvalis orcadensis*). *J Zool* **247**, 371–379. (doi:10.1111/J.1469-7998.1999.TB01000.X)

68. Roth TC, Lima SL. 2007 The predatory behavior of wintering Accipiter hawks: Temporal patterns in activity of predators and prey. *Oecologia* **152**, 169–178. (doi:10.1007/S00442-006-0638-2)

69. Harmsen BJ, Foster RJ, Silver SC, Ostro LET, Doncaster CP. 2011 Jaguar and puma activity patterns in relation to their main prey. *Mammalian Biology* **76**, 320–324. (doi:10.1016/J.MAMBIO.2010.08.007)

70. Brown JS, Kotler BP, Smith RJ, Wirtz WO. 1988 The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia* **76**, 408–415. (doi:10.1007/BF00377036)

71. Abramsky Z, Strauss E, Subach A, Kotler BP, Riechman A. 1996 The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia* **105**, 313–319. (doi:10.1007/BF00328733)

72. Lima SL, Bednekoff PA. 1999 Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. *Am Nat* **153**, 649–659. (doi:10.1086/303202)

73. Glass TW, Breed GA, Robards MD, Williams CT, Kielland K. 2021 Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore. *Anim Behav* **175**, 163–174. (doi:10.1016/J.ANBEHAV.2021.02.017)

74. Halle S. 1993 Diel Pattern of Predation Risk in Microtine Rodents. *Oikos* **68**, 510. (doi:10.2307/3544919)

75. Roulin A. 2020 *Barn Owls*. Cambridge University Press. (doi:10.1017/9781316694114)

76. Tatler J, Currie SE, Cassey P, Scharf AK, Roshier DA, Prowse TAA. 2021 Accelerometer informed time-energy budgets reveal the importance of temperature to the activity of a wild, arid zone canid. *Mov Ecol* **9**, 1–12. (doi:10.1186/S40462-021-00246-W)

77. Cotton CL, Parker KL. 2011 Winter activity patterns of northern flying squirrels in sub-boreal forests. *Can J Zool* **78**, 1896–1901. (doi:10.1139/Z00-137)

78. Murray IW, Smith FA. 2012 Estimating the influence of the thermal environment on activity patterns of the desert woodrat (*Neotoma lepida*) using temperature chronologies. *Can J Zool* **90**, 1171–1180. (doi:10.1139/Z2012-084)

79. Van Walsum TA, Perna A, Bishop CM, Murn CP, Collins PM, Wilson RP, Halsey LG. 2020 Exploring the relationship between flapping behaviour and accelerometer signal during ascending flight, and a new approach to calibration. *Ibis* **162**, 13–26. (doi:10.1111/ibi.12710)

80. Schalcher K. 2023 The use of high throughput wildlife tracking technology to study multiple aspects of barn owl movement ecology. PhD Thesis, University of Lausanne.

81. Strandberg R, Alerstam T, Hake M. 2006 Wind-dependent foraging flight in the Osprey *Pandion haliaetus*. *Ornis Svec* **16**, 150–163. (doi:10.34080/os.v16.22711)

82. Shepard ELC, Ross AN, Portugal SJ. 2016 Moving in a moving medium: new perspectives on flight. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**. (doi:10.1098/RSTB.2015.0382)

83. Jakosalem PGC, Collar NJ, Gill JA. 2013 Habitat selection and conservation status of the endemic Ninox hawk-owl on Cebu, Philippines. *Bird Conserv Int* **23**, 360–370. (doi:10.1017/S0959270912000317)

84. Cherry MJ, Barton BT. 2017 Effects of wind on predator-prey interactions. *Food Webs* **13**, 92–97. (doi:10.1016/J.FOOWEB.2017.02.005)

85. Ullmann W, Fischer C, Kramer-Schadt S, Pirhofer-Walzl K, Eccard JA, Hardert A, Sliwinski K, Crawford MS, Glemnitz M. 2022 The secret life of wild animals revealed by accelerometer data: How landscape diversity and seasonality influence the behavioural types of European hares. *Res Sq* (doi:10.21203/RS.3.RS-1621148/V1)

86. Gorini L, Linnell JDC, May R, Panzacchi M, Boitani L, Odden M, Nilsen EB. 2012 Habitat heterogeneity and mammalian predator–prey interactions. *Mamm Rev* **42**, 55–77. (doi:10.1111/J.1365-2907.2011.00189.X)

87. Kullberg C. 1995 Strategy of the Pygmy Owl while hunting avian and mammalian prey. *Ornis Fenn* **72**, 72–78.

88. Jacob J, Manson P, Barfknecht R, Fredricks T. 2014 Common vole (*Microtus arvalis*) ecology and management: implications for risk assessment of plant protection products. *Pest Manag Sci* **70**, 869–878. (doi:10.1002/PS.3695)

89. Janova E, Heroldová M. 2016 Response of small mammals to variable agricultural landscapes in Central Europe. *Mammalian Biology* **81**, 488–493. (doi:10.1016/j.mambio.2016.06.004)

90. Fischer C, Schröder B. 2014 Predicting spatial and temporal habitat use of rodents in a highly intensive agricultural area. *Agric Ecosyst Environ* **189**, 145–153.

91. Aschwanden J, Holzgang O, Jenni L. 2007 Importance of ecological compensation areas for small mammals in intensively farmed areas. *Wildlife Biol* **13**, 150–158. (doi:10.2981/0909-6396)

92. Jacob J. 2003 Short-term effects of farming practices on populations of common voles. *Agric Ecosyst Environ* **95**, 321–325.

93. Jacob J. 2008 Response of small rodents to manipulations of vegetation height in agro-ecosystems. *Integr Zool* **3**, 3–10. (doi:10.1111/J.1749-4877.2008.00078.X)

94. Norberg RA. 1981 Temporary Weight Decrease in Breeding Birds May Result in More Fledged Young. *Am Nat* **118**, 838–850. (doi:10.1086/283874)

95. San-Jose LM *et al.* 2019 Differential fitness effects of moonlight on plumage colour morphs in barn owls. *Nat Ecol Evol* **3**, 1331–1340. (doi:10.1038/s41559-019-0967-2)

96. Chimienti M, Cornulier T, Owen E, Bolton M, Davies IM, Travis JMJ, Scott BE. 2016 The use of an unsupervised learning approach for characterizing latent behaviors in accelerometer data. *Ecol Evol* **6**, 727–741. (doi:10.1002/ECE3.1914)

Chapter 3:

Individual quality and environmental factors interact to shape reproduction and survival in a resident bird of prey

Chapter 3

Individual quality and environmental factors interact to shape reproduction and survival in a resident bird of prey

Roman Bühler[1,2], Thomas V. Riecke[1,3], Kim Schalcher[2], Robin Séchaud[1,2], Alexandre Roulin[2] and Bettina Almasi[1]

[1]Swiss Ornithological Institute, Seerose 1, CH-6204, Sempach, Switzerland.

[2]Department of Ecology and Evolution, University of Lausanne, Building Biophore, CH-1015, Lausanne, Switzerland.

Chapter Status:
Submitted to: Proceedings B

Authors contributions:

All authors designed the project, A. R. and B. A. funded the research. R. B. and K. S. collected data. R. B., T.V.R. and B. A. analysed data. R. B. wrote the manuscript, with significant contributions of all co-authors.

Abstract

Investigating among-individual differences in reproductive success and survival is essential for understanding eco-evolutionary processes. We used five years of demographic data from 556 breeding barn owls (*Tyto alba*) to estimate associations between intrinsic and extrinsic covariates on survival and reproduction throughout the annual cycle. As males and females have distinct roles in reproduction, environmental conditions and individual quality may be differentially linked to their fitness at different timepoints. Males breeding early and inhabiting prey-rich areas experienced higher reproductive success but faced greater reproductive costs. Indeed, the number of offspring a male cared for was negatively associated with body condition and survival. However, our results indicate that these influences can be mitigated in males experiencing favourable post-breeding environmental conditions. For female owls, early breeding and high food availability during the breeding period was linked with increased reproductive success. Prey availability during incubation and higher reproductive output was associated with higher survival into the next breeding period in females. Unlike males, females did not exhibit obvious trade-offs between reproductive success and survival. Our research demonstrates trade-offs between fecundity and survival, and that females paired with males able to provide sufficient food experience higher survival and reproduction.

Introduction

Investigating variation in reproductive success and survival is essential for understanding eco-evolutionary processes and population dynamics [1,2]. Rearing offspring is one of the most energetically costly activities for adult birds [2,3] and depending on their parental role the consequences of reproduction and the trade-off between reproductive effort and survival may differ for males and females [4].

Both intrinsic (individual specific, e.g., age, phenotype) and extrinsic (environment specific, e.g., resource availability, meteorological conditions) factors influence individual fitness (survival and reproduction). Food availability directly influences individual fitness and the timing of the annual life cycle. During the non-breeding period, food availability plays a critical role in determining the fitness of animals, as they need to meet their energy requirements for survival [5,6] and accumulate resources in preparation for the upcoming breeding investment [7,8]. Food availability before breeding can influence timing of breeding, by influencing arrival time at the breeding grounds [9,10] and the timing of brood initiation [7,11,12]. The availability of food can influence initial investment via clutch size [12–15] as well as reproductive success [16–18]. Energy derived from resources is limited and must be allocated to different activities during the annual life cycle [2,3]. Consequently, a high energy investment in reproductive effort for a given breeding attempt is expected to trade-off with survival [3,19,20] or with subsequent breeding attempts within [21–24] or among years [25,26]. Therefore, food availability can influence individual fitness either directly through survival perspectives or indirectly via reproductive costs.

Intrinsic factors also drive variation in individual fitness, as well as individual responses to extrinsic factors [23,27–29]. Indeed, it is often observed that some individuals consistently outperform others, e.g., individuals with a higher breeding success also have a higher survival in any environmental context [30–32]. These differences in individual performance are generally rooted in intrinsic differences which are shaping their life-history strategies [2]. The most well-known intrinsic factors that can lead to different responses (i.e., life history trade-offs) to the same environmental stressors are sex and age [2], but there are other measurable intrinsic factors which are correlated with individual quality. For example, genetically determined melanin-based coloration is frequently reported to signal differences in quality which can result in alternative life history strategies [33,34]. In the barn owl (*Tyto alba*), females with large melanic spots on their plumage (which has a genetic basis, [35]) breed at younger age, have higher survival rates [36], and increased lifetime reproductive success [37].

Another measurable intrinsic factor that affects individual fitness is how individuals react under environmental pressure. Glucocorticoid hormones (GCs) are important mediators between an organism and its environment, enabling appropriate physiological and behavioural responses to environmental perturbations. Basal GC levels are responsible for the maintenance of energy homeostasis in response to energetic demands [38,39]. GCs are also part of the adrenocortical stress response, which controls the reallocation of resources to physiological functions important for self-preservation and survival when the environment becomes unpredictably challenging. It follows that GCs play an essential role in mediating trade-offs between different life history traits and can therefore be associated with fitness components [40–43].

Identifying the factors that influence individual fitness requires detailed data on both individual performance and environmental conditions. The development and miniaturisation of tracking devices makes it possible to equip small animals and to track them over long periods of time [44]. Such devices can be used to track animal movements, determine time of death, and locate breeding sites. Combined with traditional capture-recapture and breeding success data, this allows a detailed assessment of factors that influence individual fitness in a species with biparental care. In the present study, we investigated how prey availability and intrinsic factors are related to breeding success and annual survival. Prey availability varies greatly throughout the year [45], and a key aim of the study is to investigate at what point in the annual cycle prey availability most strongly influences annual breeding success and survival, and whether these associations differ between sexes. A secondary aim is to investigate whether breeding success imposes reproductive costs on survival, and whether these costs are similar for males and females.

We use a five-year (2017-2021) capture-reencounter dataset of 556 individuals of the Western barn owl, combined with information on reproductive success, prey availability in its preferred hunting habitat [45,46] and individual quality measures such as sex, experience, GC levels, and plumage colouration. We used a hierarchical model incorporating live-dead encounter and fecundity data to estimate the direct and indirect links between intrinsic and extrinsic covariates and survival and reproductive performance [47]. The barn owl is a resident bird of prey that produces one to two broods per year, depending on environmental conditions [48]. As the barn owl is an income breeder, we expect the onset of reproduction and the annual number of eggs to depend on prey availability during the early breeding period [49,50], while the annual number of fledglings is likely to depend mainly on environmental conditions during the brood-rearing period. In barn owls, survival is known to be strongly dependent on winter severity, with cold temperatures increasing energy requirements and persistent snow cover reducing prey accessibility [6]. Less detrimental effects such as prey availability during the non-breeding period and reproductive costs are less well understood and will be investigated in this study.

Material and Methods

Study area and study population

We studied barn owls in western Switzerland (46°49'N, 06°56'E) in an area of ~1,000 km^2 characterized by intensive agriculture and interspersed with villages and forests. The area can be divided into four geographical regions (plain of Orbe, plain of the Broye, Haut-Fribourg, Gros de Vaud) slightly differing in terms of topography and land use [45]. More than 400 nest boxes for barn owls have been installed throughout the study area since 1985. *Arvicola, Microtus,* and *Apodemus* species represent the staple prey of our study population of barn owls, but other small mammals serve as suitable prey as well [51,52]. The breeding season extends from February to October [53] and is followed by a resident wintering period.

Individual data

Once a breeding attempt was detected in a nest box, standard monitoring involved four visits per brood: A first visit just before hatching to determine clutch size, second and third visits when the oldest nestling was 25 and 35 days old, and a final visit when the oldest nestling was close to fledging, around 55 days old. Breeding adults were captured at the nesting site and data on body mass, age, plumage traits and sex were collected for each captured adult. Sex was identified by the presence (female) or absence (male) of a brood patch. The age of each animal was determined from previous encounters or via primary and secondary moult patterns; this allowed us discrimination between a bird in its second year of life (when there is no moult) or an older bird (which shows moulted feathers; [54]). Eumelanin spottiness of plumage was assessed by measuring spot diameter (to the nearest 1/10 mm) of 10 spots on the belly and the breast. Body mass of breeding adults was measured at different timepoints: shortly before hatching, 25 days after hatching and 35 days after hatching. Clutch size, number of nestlings and fledglings were recorded for each breeding attempt. Number of nestlings refers to the number of juvenile birds alive at the visit 25 days after hatching and number of fledglings was defined as number of nestlings reaching an age of 55 days. Whenever possible, two blood samples per adult were taken to determine GC concentration (baseline: within 3 min of capturing event; [55], stress-induced: after 25 min of handling). GC concentration was analysed following procedures described in [56]. Depending on the concentration of the internal control and the year of analysis, intra-assay variation ranged from 5 to 18 % (mean 11.4 ± 3.8 %) and inter-assay variation from 11 to 28 % (mean: 19.6 ± 5.7 %).

The final dataset included 556 different breeding adults captured in our study area between 2017 and 2021. Out of 556 individuals (257 males and 299 females), 237 individuals (130 males and 107 females) were equipped with a GPS transmitter (Technosmart, Italy), as well as a lightweight VHF transmitter (µTag, Swiss Ornithological Institute). Owls were either directly captured at their nest site during the day, or at night by using sliding door traps. The attached GPS/VHS tag combination weighted <13 g (which is <5% of body mass, mean body mass before tagging: 297 g, range: 260-440 g). Tags were attached with spectra-tubular filament (4.7 mm, polyethylene, Producer: Bally Ribbon Mills, US) using a wing loop harness. The VHF transmitters were programmed to send signals during a single, synchronized week the following spring. During this time, we intensively searched inside the study area to check status of marked individuals (alive, dead, or unknown/no signal detected). VHF equipped birds were expected to have higher dead-recovery as well as higher recapture probability, as detection was not dependent on physically capturing alive individuals or finding dead birds by chance. All manipulations were performed under authorization from the Department of Consumer and Veterinary Affairs (VD and FR 2844 and 3213) and the Federal Office of Environment.

Prey availability

Prey availability was monitored throughout the year using two indirect methods: Fresh signs of voles (heaps, holes, and runways of *Arvicola sp.* and *Microtus sp.*) were counted along 5x1m transects [57], and above ground activity of all small mammal species was assessed by placing a plastic plate covered with a thin layer of graphite during two consecutive nights along each transect (adapted from [58]). The number of characteristic tracks of small mammals walking across the plates were then counted [59]. Combining both methods, we obtained an index for the activity density of voles and total small mammals. The two activity density indices were recorded in the four geographical regions of our study area, with four 9 km^2 subplots selected in each region. Indices were counted six times per year at two-month intervals in four different habitat types: crop-rotation (annual crop), grasslands (intensive and extensive grassland), border structures (1m margin along roads), and biodiversity structures (hedges and wildflower areas). Nine transects were walked, and nine plates were laid in each habitat type during each counting period. This resulted in a total of 576 transects and an equal number of plates for each 2-month period (details in [45]).

Both methods of assessing prey availability have been shown to correlate well with estimates of relative abundance from live trapping [58,60]. In addition, vole populations in Central Europe have been shown to fluctuate synchronously across large spatial scales [61]. To obtain estimates of the two activity indices on a continuous time scale for voles (transect method, hereafter vole activity density index) and small mammals (track-plate method, hereafter small mammal activity density index) separately, two generalized additive mixed models were fitted [45].

Habitat composition

To estimate prey availability in the preferred hunting habitats [45,62], habitat composition within a radius of 1.5 km (average home-range of adult barn owls in our study area; [45,56,62]) around each breeding site was recorded once in summer and once in winter, with the assumption of that adult birds stay close to breeding site in winter [45]. Land use information was collected from cantonal offices (canton of Vaud: all agricultural land, canton of Fribourg: permanent perennial crops only) and complemented with habitat mapping in the field. Information on coverage of urban area, hedges, single trees, roads (roads, highways, railways) and border structures (1m buffer around roads, highways and railways) were obtained from the TLM3D database of the Swiss federal office of topography (TLM3D, resolution: 0.2-3m, Bundesamt für Landestopografie Swisstopo). When data on coverage of habitats were still missing, information from the previous year was used as a proxy to fill the information gaps (correlation between years: 0.8-1 depending on habitat type).

Statistical analysis

Treatment of covariates

Experience was defined as 0 if individuals were first time breeders or 1 if they had already attempted to reproduce at least once. Laying date was defined as day of the year when the first egg of the first brood was laid. Body condition index was estimated during incubation and during brood-rearing period by fitting a linear regression for each of the two timepoints using body mass as the response and wing length, time of the day of capture and sex as explanatory variables. The residuals of the linear regressions were then used as a proxy for body condition, thereby correcting for individual body size [63]. Total prey activity density for all small mammals, hereafter small mammal activity density, and voles, hereafter vole activity density of each of the four habitat types (crop-rotation, grassland, biodiversity structures, boundary structures) available within 1.5 km of the last breeding site was calculated by multiplying the activity density index of a habitat type at one of five different times (pre-laying, breeding, rearing, early and late winter) by the corresponding area. The number of eggs, nestlings and fledglings was summed up for each adult and each year (Supp. mat. S3). Depending on the year, the proportion of individuals performing a second brood varied between 6 to 21%. Of these individuals who performed a second brood, around 69% where females and 31% males. GC concentration and the diameter of plumage spots were included as measured numerical values. Missing covariates were estimated from a normal distribution with population-, individual- or sex-specific mean and standard deviation depending on the type of covariate. (For details see supp. mat. S1)

Hierarchical model

We estimated the effects of intrinsic (i.e., body condition, experience) and extrinsic (i.e., prey availability) covariates on the annual number of eggs laid, hatching success, fledging success, and survival using a path analysis [47]. In this way, we were able to estimate both the direct and indirect relationships between various environmental and individual covariates on survival and fecundity over the annual cycle (Figure 1).

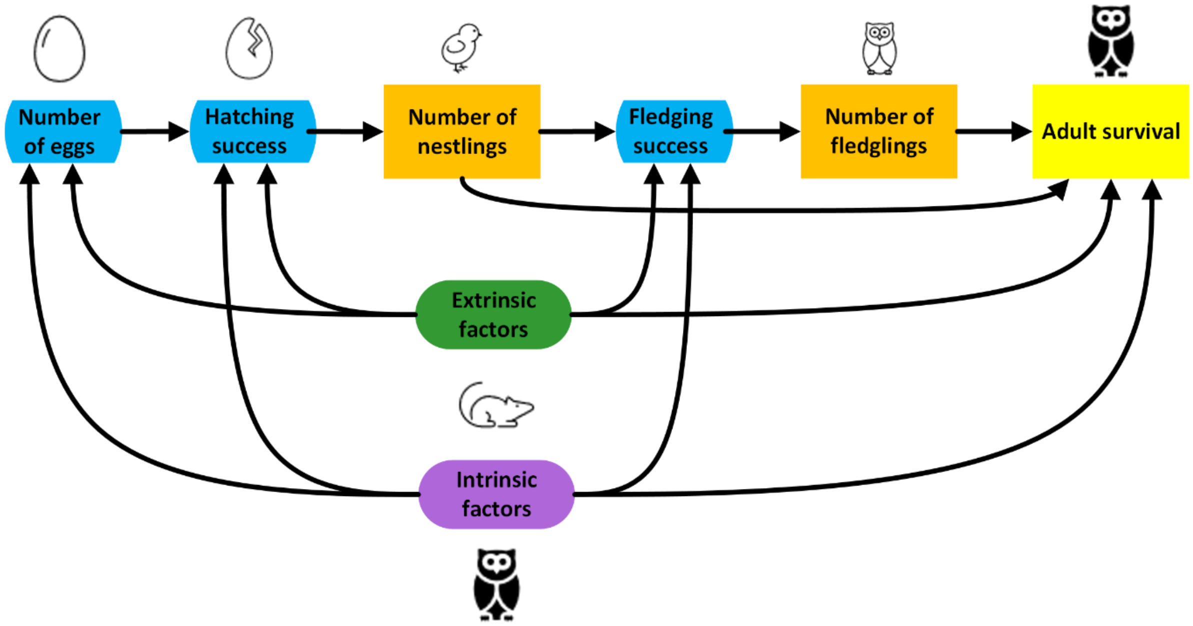


Figure 1: A simplified directed acyclic graph demonstrating the modelled relationships between intrinsic (red) and extrinsic (green) covariates on various components of reproductive success (blue) and adult survival (yellow), as well as the relationships between reproductive investment and success (orange) on survival.

First, we modelled the number of eggs laid during each breeding season by each individual as a function of adult experience, laying date and pre-laying small mammal activity density and vole activity density using Poisson regression. Second, we modelled the annual number of nestlings reared by each individual as the outcome of a Binomial trial given the number of eggs, and the modelled hatching success. Hatching success was modelled as a function of adult experience, the number of eggs laid, laying date, adult body condition measured during incubation, and small mammal activity density and vole activity density during incubation.

We then modelled the annual number of fledglings produced by each individual as the outcome of a Binomial trial given the number of nestlings, and the estimated fledging success. Like hatching success, fledging success was modelled as a function of adult experience, number of nestlings, laying date, adult body condition measured during brood-rearing and small mammal activity density and vole activity density during brood-rearing.

To estimate recapture (p), recovery (r), and survival (φ) probability, a mark-recapture-recovery model was used [64,65]. Survival probability was modelled as a function of sex and adult experience, adult body condition measured during brood-rearing, number of nestlings, number of fledglings, baseline GC concentration, stress-induced GC concentration, spot diameter of plumage and small mammal activity density and vole activity density during both the incubation period and early winter. We modelled recapture probability and recovery probability separately for the ring-only and the GPS-VHF groups, as we were more likely to encounter individuals marked with active GPS-VHF transmitters (see supp. mat. S2, S4 for additional details).

The model was fit in JAGS [66] using the jagsUI package [67] in R 4.2.1 [68]. Before incorporating variables into the model, they were checked for correlation (<0.7), scaled, and centred. We sampled 250,000 iterations with four chains with a burn in of 100,000 iterations and retained every 25th iteration. We checked that $\hat{R}$ values of posterior distributions were less than 1.01, and visually inspected trace plots to check for convergence [69]. In the results, we report the median of the posterior distribution together with the 95% credible intervals (CI), as well as the proportion of the posterior distribution on the same side of zero as the mean (f).

Results

Number of eggs

Higher annual number of eggs were produced by females (Figure 2 and 4, Supp. mat. S6) with earlier first clutches ($\beta= -0.24$) and higher small mammal activity density prior to laying ($\beta=0.09$). High vole activity density prior to laying was linked to lower annual number of eggs produced ($\beta= -0.04$). Experience of the female was weakly but positively related to the annual number of eggs ($\beta=0.06$).

Males showed a similar pattern with laying date and small mammal activity density being associated with the annual number of eggs to which the male contributed (Figure 2 and 5, Supp. mat. S6). Earlier first clutches ($\beta= -0.10$) and increased small mammal activity density ($\beta=0.06$), were related to a higher annual number of eggs. Contrary to the results found for females, vole activity density was not strongly associated with annual number of eggs ($\beta= -0.02$). In males, experience was linked with lower number of eggs per year ($\beta= -0.06$).

Hatching success

In females, hatching success (Figure 2 and 4, Supp. mat. S7) was positively related to high vole activity density during incubation of the first clutch ($\beta=0.22$), early laying of the first clutch (β= −0.39), and high female body condition index after laying the first clutch (β=0.23). High number of annually produced eggs were associated with lower hatching success (β= −0.48) but positively associated with experience (β=0.15). However, small mammal activity density was not related to hatching success.

In males, hatching success (Figure 2 and 5, Supp. mat. S7) was positively linked with high male body condition after laying (β=0.35) and high vole activity density during incubation (β=0.09). Experience was associated with higher overall hatching success (β=0.18) but was also linked with lower annual number of eggs (β= −0.32). Small mammal activity density and laying date did not seem to be related to hatching success.

Fledging success

In females, fledging success (Figure 2 and 4, Supp. mat. S8) was negatively related to the number of nestlings (β= −0.20) and positively associated with body condition during the brood-rearing period (β=0.10). No strong evidence was found for a relationship between fledging success and female experience, laying date or small mammal activity density, as well as vole activity density during the brood-rearing period.

In males, body condition during the brood-rearing period was positively related to fledging success (Figure 2 and 5, Supp. mat. S8). Annual fledging success was negatively linked with body condition during the brood-rearing period of the first brood (β= −0.15). Fledging success was negatively linked to the number of nestlings the male contributed to annually (β= −0.20). Vole activity density and small mammal activity density during the brood-rearing period as well as laying date and experience of the male were not linked with fledging success.

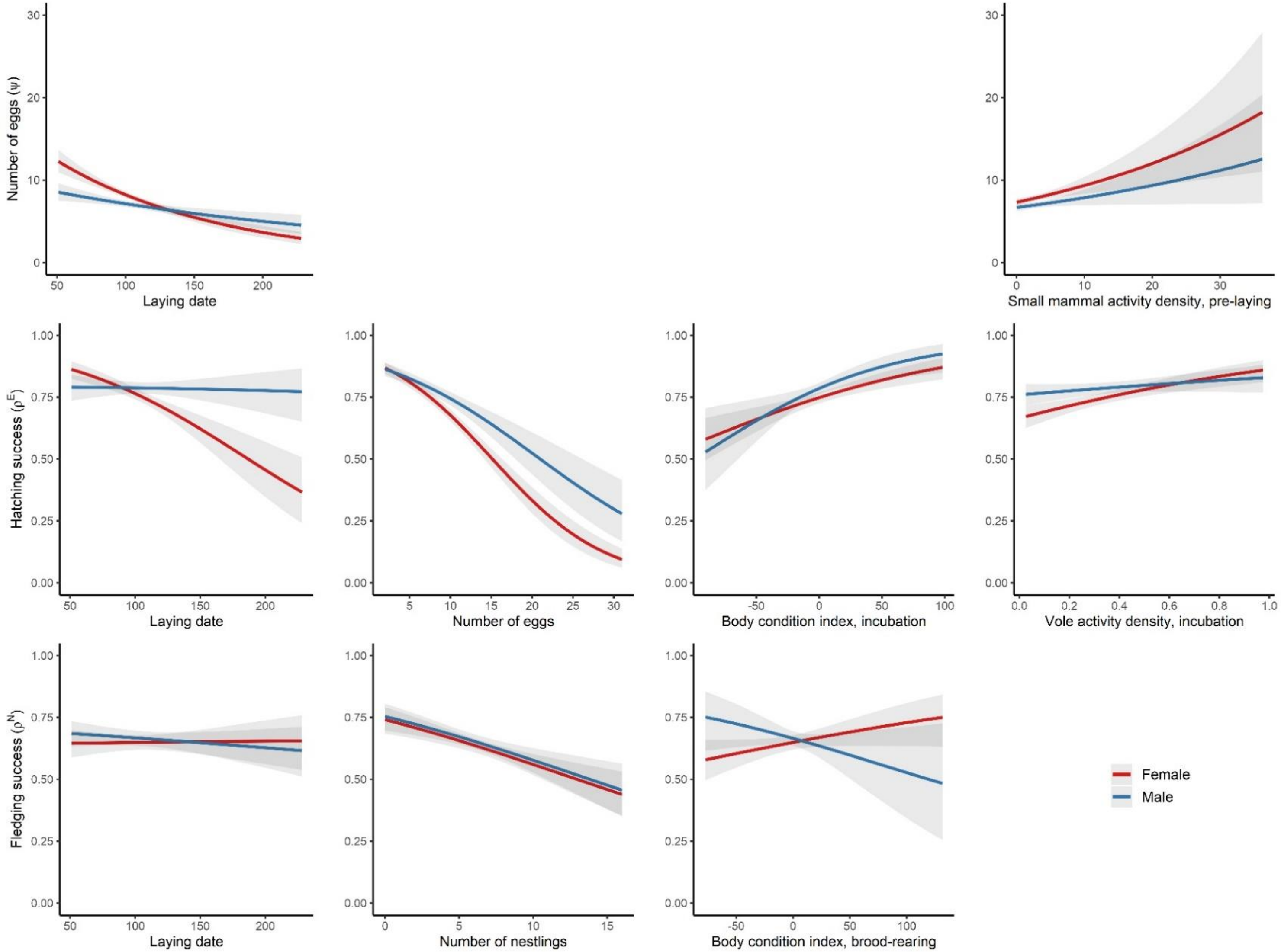


Figure 2: Mean estimates (solid lines) and 95% credible intervals (shaded area) of the relationship between annual number of eggs (ψ), hatching success (ρ^E), fledging success (ρ^N) and explanatory variables. Females are presented in red and males in blue. Estimates, presented for experienced individuals based on the models presented in supplementary material S6/S7/S8.

Survival of adults

Female survival (Figure 3 and 4, Supp. mat. S9) was positively related to annual number of fledglings produced (β=0.44). Furthermore, females with larger spot diameter on belly and breast were associated with higher survival compared to those with smaller spot diameters (β=0.25). There was a negative link of high baseline GC on female survival (β= –0.20). Small mammal activity density during incubation was positively related with female survival (β=0.28), while vole activity density during incubation and small mammal activity density and vole activity density during winter were not linked with survival. We found no association between female survival and experience (Supp. mat. S5), body condition measured during the brood-rearing period, number of nestlings produced, or stress-induced GC level.

Experienced males were associated with higher survival (Figure 3 and 5, Supp. mat. S9) than non-experienced males (β=0.71) (Supp. mat. S5). Like females, the diameter of plumage spots was positively linked with male survival (β=0.31). For reproductive parameters, the strongest link with male survival was observed for the number of nestlings produced during the reproductive period (β= –0.32). While vole activity density during the incubation period was negatively associated with male survival (β= –0.43), vole activity density during early winter was positively linked with survival (β=0.50). There was no support for a strong association between male survival and body condition during the brood-rearing period, number of fledglings, baseline and stress-induced GC, as well as small mammal activity density during incubation and early winter.

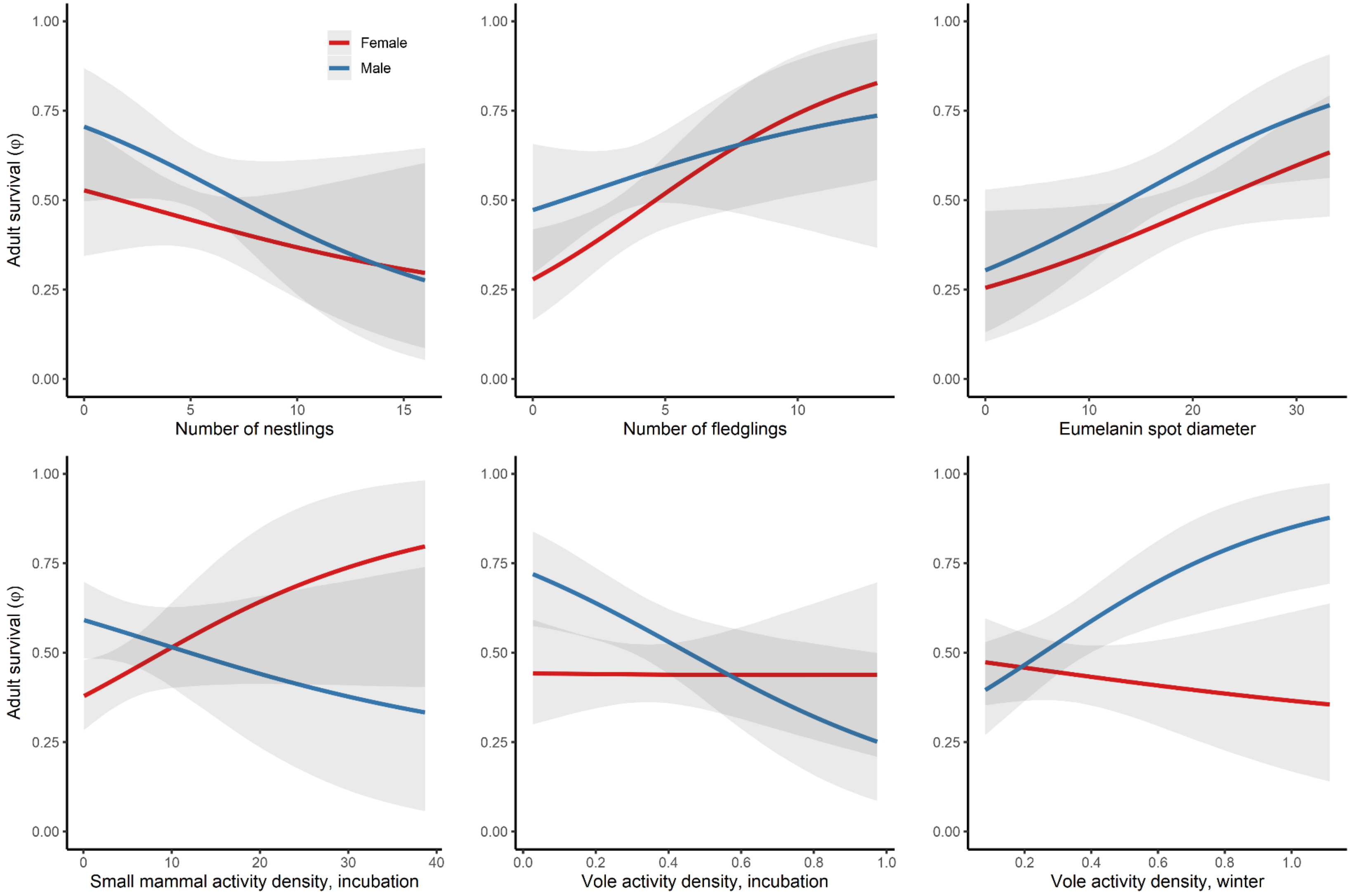


Figure 3: Mean estimates (solid lines) and 95% credible intervals (shaded area) of the relationship between adult survival (φ) and explanatory variables. Females are presented in red and males in blue. Estimates, presented for experienced individuals based on the model presented in supplementary material S9.

Figure 4: A directed acyclic graph demonstrating the relationships of intrinsic (red) and extrinsic (green) covariates on female reproductive success (blue) and survival (yellow). Estimates and f-values (in brackets) are derived from the models shown in supplementary material S9 and are based on 556 individuals over 5 years. Bold arrows indicating f values >0.975, solid lines f values between 0.9 and 0.974 and dashed lines values <0.9.

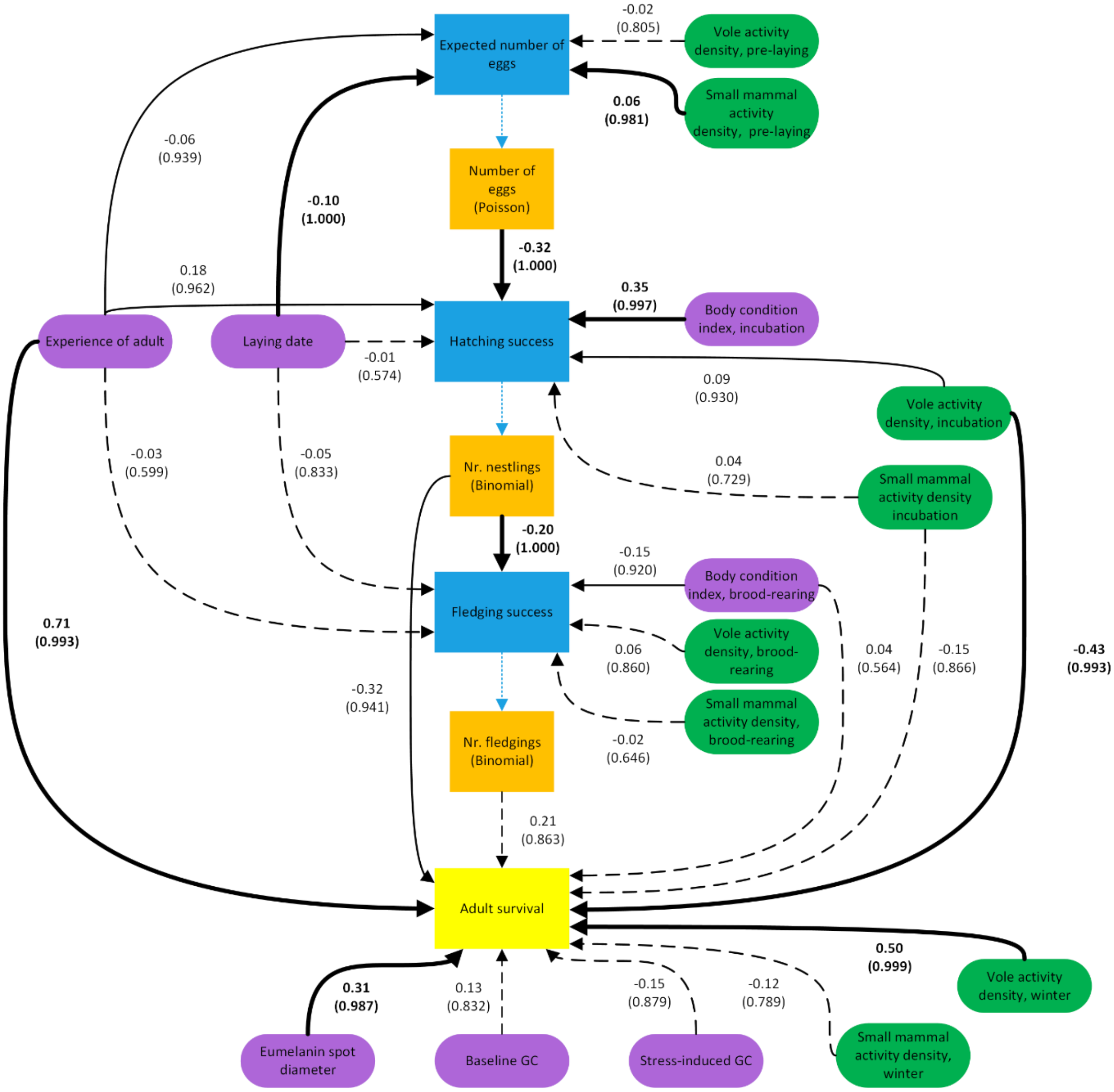


Figure 5: A directed acyclic graph demonstrating the relationships of intrinsic (red) and extrinsic (green) covariates on male reproductive success (blue) and survival (yellow). Estimates and f-values (in brackets) are derived from the models shown in supplementary material S9 and are based on 556 individuals over 5 years. Bold arrows indicating f values >0.974, solid lines f values between 0.9 and 0.974 and dashed lines values <0.9.

Discussion

Males and females often have distinct roles in reproduction, which means that workloads may be greatest at different times during reproduction. Depending on sex and timing, environmental factors have different effects on fitness. Our study reveals that both environmental conditions and factors indicting individual quality can directly and indirectly affect adult survival. Depending on reproductive stage and sex, prey availability and individual quality factors were also differently associated with reproduction. Overall, males faced a trade-off between reproduction and survival, while female survival and reproduction were primarily influenced by female quality and environmental conditions. Below, we delve into how the examined intrinsic and extrinsic factors were related to reproductive performance and survival.

Extrinsic factors and reproduction and survival

In this study, we examined the impact of pre-breeding and breeding season food availability, as well as brood timing, on annual reproductive success and survival. High prey availability early in the breeding season resulted in greater reproductive success for early breeding males. However, the more offspring they reared and the more food they had, the lower their subsequent survival, suggesting reproductive costs. In contrast, females benefited from abundant prey early in the breeding season as they could lay more eggs throughout the reproductive period and achieve higher hatching success and subsequent survival. These different relationships between food availability and reproductive success and survival are likely due to the different roles of males and females in the reproductive system.

Egg production and incubation require significant energy expenditure from female birds [70–73] including barn owls, where females exclusively incubate [49,74]. Increased small mammal activity density during incubation may therefore meet the females' energetic needs, supporting egg production, body condition maintenance and recovery from the investment, leading to enhanced female survival. Male barn owls are the only food provider for females and nestlings during incubation and early brood rearing stages [74], as females do not contribute to food provisioning until late brood-rearing [75]. Male provisioning of food therefore increases the female's nest attentiveness during incubation [76,77], positively influencing hatching success [70,78,79] and reducing the risk of early brood reduction [74]. High vole activity density during incubation may therefore enable males to provide sufficient prey during this period, leading to improved hatching success and sustained female body condition.

The peak investment for males, however, is expected to happen during the brood-rearing phase when males are the main provider of food to the nestlings [75]. Because of these differences in peak investment in reproduction, it is likely that different environmental cues are used by females and males at different times to guide their investment in reproduction [80]. For female barn owls, food availability before egg laying and during incubation was related to reproductive success and survival. In contrast, male reproductive success is mainly linked with food availability during brood-rearing. However, high investment during brood-rearing was negatively associated with male survival, particularly when prey was abundant early in the breeding season. Prey availability during incubation seemed to influence male survival through two distinct pathways. Firstly, high vole activity density during incubation of the first brood was positively associated with overall hatching success, leading to a subsequent increase in the number of nestlings, which is again negatively linked with male survival. Thus, we observed an indirect negative link of prey availability during incubation on male survival mediated by reproductive effort. Additionally, vole activity density during incubation was directly negatively associated with survival. This suggests that males incur certain costs associated with high vole activity density during incubation not reflected in the number of nestlings. Higher prey availability earlier in the season may lead to increased and/or early investment by males, such as energy demanding courtship behaviour [81]. This investment may not be fully mirrored by the number of nestlings but would manifest as a direct negative link of vole activity density during incubation on male survival. The extent to which the discussed costs influenced males seemed to depend on the environmental conditions experienced after the breeding season. High prey availability in early winter (represented by high vole activity density) may help males recover from the energy-demanding breeding period, therefore positively acting on survival.

Timing of the first clutch was linked with annual number of eggs the sexes contributed to as well as with hatching success for females. Birds breeding early and under good conditions might either lay larger first clutches and/or have a higher probability to produce a second clutch. Birds in seasonal environments face time constraints and only birds reproducing early can start a successful second breeding attempt [48,53,82,83]. Early food availability may allow earlier and more successful first breeding, while also providing the necessary energy and time to initiate a second brood

[84]. In barn owls, late and second clutches are usually larger than early and first clutches [52,62,85] suggesting that the observed link emerged from double brooding rather than from increased clutch size during first reproduction. Females exhibited a stronger association between laying date, the number of eggs, and hatching success compared to males, potentially attributed to the nearly two times higher rate of second brood initiation in females (Supp. mat. S3).

Early food availability may promote early laying, but whether birds engage in double brooding depends on food availability later in the season as well. Early prey availability may serve as an indicator of favourable conditions later in the season. High small mammal activity density is likely to reflect increased availability of mobile *Apodemus sp.* [59]. These prey species tend to move from forests and hedges into arable fields as the seasons progress [86], which are the preferred hunting areas for barn owls [46]. Consequently, early high small mammal activity density can positively influence the first breeding attempt and increase the likelihood of a second breeding event, resulting in a higher number of eggs per breeding season. In fact, studies on female barn owls have demonstrated a correlation between the availability of *Apodemus sp*. in early-season food stores and the initiation of a second brood [48]. The connection between a decreasing annual number of eggs and high vole activity density prior to egg-laying may have a similar underlying cause. Early high vole activity density could indicate an initial peak in vole populations, which may initially seem advantageous. However, vole populations with high densities early in the year are susceptible to population crashes later in the season [87]. These crashes can have negative implications for the initiation of second broods, as resource availability later in the season becomes crucial for successful breeding attempts [84,88].

Intrinsic factors and reproduction and survival

We measured the effects of experience of an individual (first year breeders versus older individuals), their melanin-based colouration, body condition and the stress hormone GC on different demographic components. All these four intrinsic quality measurements were positively linked with aspects of reproductive success and survival in both sexes. In males, a reproductive conflict arises between maximizing offspring numbers, which has a negative impact on body condition [89], and ensuring good survival, which is positively associated with body condition. Increasing current reproductive output at the cost of future fitness (survival and future reproduction) is an observed strategy in avian species

[90–92]. Male body condition showed a positive association with hatching success, but there was a trade-off observed between self-maintenance and reproductive success [3,93]. Males in better body condition produced a greater number of nestlings, but this came at the cost of lower survival and decreasing body condition. It appears that barn owl males make sacrifices in their body condition to enhance their reproductive success, although they may have a limit on how much they are willing to jeopardize future reproduction [62].

Experience in reproductive tasks, breeding habitat selection, and familiarity with the surroundings can positively influence the reproductive performance of birds. Experienced, high-quality, individuals are more likely to acquire and efficiently utilize good habitat [94–96] mate with a better compatible partner [19,97], start breeding early in the season [19,52,98] and have higher reproductive output [19,98], implying a high probability to produce a second annual brood [53]. In our study experienced females had more eggs and a higher hatching success than inexperienced females, while experienced males cared for fewer eggs than inexperienced males. Experienced individuals start breeding earlier in the season when clutches are typically smaller [52,62,85] and the probability of producing a second clutch also increases with age in barn owls [48,99]. For females, the sex with the higher probability of producing a second annual clutch, breeding early allows them to produce a second annual clutch. Experienced males, on the other hand, seem to compensate for the fewer eggs by having clutches with higher hatching success. Eggs from females which are in good condition during incubation and brood-rearing not only have high hatching success but also high fledgling success. This suggests that females, unlike males, do not compromise their body condition to achieve high reproductive success.

Female reproductive performance appears to depend on her intrinsic quality and the performance of her mate [100,101]. High-quality males may enable females to breed earlier, achieve higher hatching success, maintain better body condition, and produce more fledglings. When males provide sufficient food during incubation, females do not need to hunt and can consistently incubate, leading to higher hatching success [74] without compromising their own body condition [76,77,102]. Additionally, increased brood care from the male could enable the female to initiate a second breeding attempt earlier [53,103]. Reproducing with high quality males would therefore result in high number of offspring under proportionally lower female workload, probably explaining the increased survival of females with increasing number of produced fledglings.

In our study, experienced males show higher survival than inexperienced males. The higher survival of experienced males can be attributed to the selective pressure exerted during their first winter and first reproduction. High-quality males are more likely to survive these critical phases of selection, leading to increased survival in experienced birds in subsequent years [104]. The lack of a relationship between experience and female survival might be due to the lower selective pressure of breeding on females. Males and females with larger eumelanin-based spot diameters showed higher probability of survival than individuals with smaller eumelanin-based spots. That eumelanin coloration correlates with survival and thus represents an individual quality factor has been shown for several bird species [33,34,36,105]. In barn owls, the size of eumelanin-based spots has been consistently linked to coping abilities in stressful situations. Individuals with larger spots demonstrate better resilience in the face of food deprivation [28], increased resistance to oxidative stress [106], and a lower GC stress response during acute stress [107]. In addition, males with larger spots have been shown to be better providers when exposed to elevated GC levels [27] and females with larger spots reproduce earlier [36]. It has been suggested that elevated GC concentration in larger-spotted females leads to a behaviour shift towards self-maintenance [56], which could lead to increased survival of larger spotted individuals under challenging conditions. In line with this, our data indicate that females with lower baseline GC levels and larger spots demonstrate higher survival rates. Therefore, larger spots in barn owls appear to serve as an indicator of individual quality.

Conclusion

Our study highlights the complex relationships between individual and environmental factors, reproductive investment, and survival in barn owls. The results suggest that environmental and individual conditions can influence adult fitness through direct and indirect pathways. The strength of the associations between environmental and individual factors on survival and reproduction varies with sex and season. Prey availability determines the reproductive success of males and females, but high prey availability in early winter is especially critical for male survival. Providing habitat with sufficient prey during the non-breeding period may therefore be of uttermost importance for male survival. In addition, males experience a distinct conflict between reproduction and survival, while female survival and reproduction depend mainly on the quality of the female and environmental conditions. The study therefore emphasizes the importance of considering multiple factors and including the different pathways in which they can be associated with fitness when examining reproductive success and its link to survival.

References:

1. Begon M, Mortimer M, Thompson DJ. 2009 *Population ecology : a unified study of animals and plants*. 2nd edn. Wiley-Blackwell.
2. Stearns SC. 1992 *The Evolution of Life Histories*. Oxford, UK: Oxford University Press.
3. Williams GC. 1966 Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. *Am Nat* **100**, 687–690.
4. Cruz-Flores M, Pradel R, Bried J, González-Solís J, Ramos R. 2021 Sex-specific costs of reproduction on survival in a long-lived seabird. *Biol Lett* **17**, 20200804. (doi:10.1098/RSBL.2020.0804)
5. Siriwardena GM, Calbarde NA, Vickery JA. 2008 Farmland birds and late winter food: does seed supply fail to meet demand? *Ibis* **150**, 585–595. (doi:10.1111/j.1474-919X.2008.00828.x)
6. Altwegg R, Roulin A, Kestenholz M, Jenni L. 2006 Demographic effects of extreme winter weather in the barn owl. *Oecologia* **149**, 44–51. (doi:10.1007/s00442-006-0430-3)
7. Robb GN, McDonald RA, Chamberlain DE, Reynolds SJ, Harrison TJE, Bearhop S. 2008 Winter feeding of birds increases productivity in the subsequent breeding season. *Biol Lett* **4**, 220–223. (doi:10.1098/rsbl.2007.0622)
8. Broggi J, Watson H, Nilsson J, Nilsson J-Å. 2022 Carry-over effects on reproduction in food-supplemented wintering great tits. *J Avian Biol* **2022**, e02969. (doi:10.1111/jav.02969)
9. Saino N, Szep T, Romano M, Rubolini D, Spina F, Moller AP. 2004 Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* **7**, 21–25. (doi:10.1046/j.1461-0248.2003.00553.x)
10. Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2004 Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society, Biological sciences* **271**, 59–64. (doi:10.1098/rspb.2003.2569)
11. Eeva T, Veistola S, Lehikoinen E. 2000 Timing of breeding in subarctic passerines in relation to food availability. *Can J Zool* **78**, 67–78. (doi:10.1139/Z99-182)
12. Tortosa FS, Pérez L, Hillström L. 2010 Effect of food abundance on laying date and clutch size in the White Stork *Ciconia ciconia*. *Bird Study* **50**, 112–115. (doi:10.1080/00063650309461302)
13. Clifford LD, Anderson DJ. 2001 Food Limitation Explains Most Clutch Size Variation in the Nazca Booby. *Journal of Animal Ecology* **70**, 539–545.
14. Korpimäki E, Hakkarainen H. 1991 Fluctuating food supply affects the clutch size of Tengmalm's owl independent of laying date. *Oecologia* **85**, 543–552. (doi:10.1007/BF00323767)

15. Solonen T, Ahola K, Karstinen T. 2015 Clutch size of a vole-eating bird of prey as an indicator of vole abundance. *Environ Monit Assess* **187**. (doi:10.1007/s10661-015-4783-0)

16. Nägeli M, Scherler P, Witczak S, Catitti B, Aebischer A, van Bergen V, Kormann U, Grüebler MU. 2022 Weather and food availability additively affect reproductive output in an expanding raptor population. *Oecologia* **198**, 125–138. (doi:10.1007/s00442-021-05076-6)

17. Lindström Å, Enemar A, Andersson G, Von Proschwitz T, Nyholm NEI. 2005 Density-dependent reproductive output in relation to a drastically varying food supply: getting the density measure right. *Oikos* **110**, 155–163. (doi:10.1111/J.0030-1299.2005.13828.X)

18. Grames EM, Montgomery GA, Youngflesh C, Tingley MW, Elphick CS. 2023 The effect of insect food availability on songbird reproductive success and chick body condition: Evidence from a systematic review and meta-analysis. *Ecol Lett* **26**, 658–673. (doi:10.1111/ELE.14178)

19. Bryant DM. 1979 Reproductive Costs in the House Martin (*Delichon urbica*). *Journal of Animal Ecology* **48**, 655–675. (doi:10.2307/4185)

20. Verhulst S. 1998 Multiple breeding in the Great Tit, II. The costs of rearing a second clutch. *Funct Ecol* **12**, 132–140. (doi:10.1046/J.1365-2435.1998.00165.X)

21. Smith RD, Marquiss M. 1995 Production and costs of nesting attempts in Snow Buntings *Plectrophenax nivalis*: why do they attempt second broods? *Ibis* **137**, 469–476. (doi:10.1111/J.1474-919X.1995.TB03255.X)

22. Grüebler MU, Naef-Daenzer B. 2008 Postfledging parental effort in barn swallows: evidence for a trade-off in the allocation of time between broods. *Anim Behav* **75**, 1877–1884. (doi:10.1016/j.anbehav.2007.12.002)

23. Plard F, Arlettaz R, Schaub M. 2018 Hoopoe males experience intra-seasonal while females experience inter-seasonal reproductive costs. *Oecologia* **186**, 665–675. (doi:10.1007/S00442-017-4028-8)

24. Hansson B, Bensch S, Hasselquist D. 2000 The quality and the timing hypotheses evaluated using data on great reed warblers. *Oikos* **90**, 575–581. (doi:10.1034/J.1600-0706.2000.900315.X)

25. Nilsson JA, Svenssonn E. 1996 The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proc R Soc Lond B Biol Sci* **263**, 711–714. (doi:10.1098/RSPB.1996.0106)

26. Rivalan P, Prévot-Julliard AC, Choquet R, Pradel R, Jacquemin B, Girondot M. 2005 Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. *Oecologia* **145**, 564–574. (doi:10.1007/S00442-005-0159-4)

27. Almasi B, Roulin A, Jenni-Eiermann S, Jenni L. 2008 Parental investment and its sensitivity to corticosterone is linked to melanin-based coloration in barn owls. *Horm Behav* **54**, 217–223. (doi:10.1016/j.yhbeh.2008.02.021)

28. Dreiss AN, Henry I, Ruppli CA, Almasi B, Roulin A. 2010 Darker eumelanic barn owls better withstand food depletion through resistance to food deprivation and lower appetite. *Oecologia* **164**, 65–71. (doi:10.1007/s00442-010-1680-7)

29. Piault R, Gasparini J, Bize P, Jenni-Eiermann S, Roulin A. 2009 Pheomelanin-Based Coloration and the Ability to Cope with Variation in Food Supply and Parasitism. *Am Nat* **174**, 548–556. (doi:10.1086/605374)

30. Blums P, Nichols JD, Hines JE, Lindberg MS, Mednis A. 2005 Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. *Oecologia* **143**, 365–376. (doi:10.1007/s00442-004-1794-x)

31. Ardia DR, Clotfelter ED. 2007 Individual quality and age affect responses to an energetic constraint in a cavity-nesting bird. *Behavioral Ecology* **18**, 259–266. (doi:10.1093/beheco/arl078)

32. Wilson AJ, Nussey DH. 2010 What is individual quality? An evolutionary perspective. *Trends Ecol Evol* **25**, 207–214. (doi:10.1016/J.TREE.2009.10.002)

33. Ducrest AL, Keller L, Roulin A. 2008 Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends Ecol Evol* **23**, 502–510. (doi:10.1016/J.TREE.2008.06.001)

34. San-Jose LM, Roulin A. 2018 Toward Understanding the Repeated Occurrence of Associations between Melanin-Based Coloration and Multiple Phenotypes. *Am Nat* **192**, 111–130. (doi:10.1086/698010)

35. Roulin A, Dijkstra C. 2003 Genetic and environmental components of variation in eumelanin and phaeomelanin sex-traits in the barn owl. *Heredity (Edinb)* **90**, 359–364. (doi:10.1038/sj.hdy.6800260)

36. Roulin A, Altwegg R. 2007 Breeding rate is associated with pheomelanism in male and with eumelanism in female barn owls. *Behavioral Ecology* **18**, 563–570. (doi:10.1093/beheco/arm015)

37. Béziers P, Roulin A. 2021 Sexual maturity varies with melanic plumage traits in the barn owl. *J Avian Biol* **52**. (doi:10.1111/JAV.02715)

38. Sapolsky RM, Romero LM, Munck AU. 2000 How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr Rev* **21**, 55–89. (doi:10.1210/edrv.21.1.0389)

39. Romero LM. 2004 Physiological stress in ecology. *Trends Ecol Evol* **19**, 249–255. (doi:10.1016/j.tree.2004.03.008)

40. Bonier F, Martin PR, Moore IT, Wingfield JC. 2009 Do baseline glucocorticoids predict fitness? *Trends Ecol Evol* **24**, 634–642. (doi:10.1016/J.TREE.2009.04.013)

41. Béziers P, Korner-Nievergelt F, Jenni L, Roulin A, Almasi B. 2020 Glucocorticoid levels are linked to lifetime reproductive success and survival of adult barn owls. *J Evol Biol* **33**, 1689–1703. (doi:10.1111/JEB.13707)

42. Breuner CW, Patterson SH, Hahn TP. 2008 In search of relationships between the acute adrenocortical response and fitness. *Gen Comp Endocrinol* **157**, 288–295. (doi:10.1016/j.ygcen.2008.05.017)

43. Hau M, Ricklefs RE, Wikelski M, Lee KA, Brawn JD. 2010 Corticosterone, testosterone and life-history strategies of birds. *Proceedings of the Royal Society B: Biological Sciences* **277**, 3203–3212. (doi:10.1098/RSPB.2010.0673)

44. Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V, Hebblewhite M. 2015 The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology* **96**, 1741–1753. (doi:10.1890/14-1401.1)

45. Bühler R, Schalcher K, Séchaud R, Roulin A, Almasi B. 2023 Influence of prey availability on habitat selection during the non-breeding period in a resident bird of prey. *Mov Ecol* **11**. (doi:10.1186/s40462-023-00376-3)

46. Séchaud R, Schalcher K, Machado AP, Almasi B, Massa C, Safi K, Roulin A. 2021 Behaviour-specific habitat selection patterns of breeding barn owls. *Mov Ecol* **9**, 1–11. (doi:10.1186/s40462-021-00258-6)

47. Gimenez O, Anker-Nilssen T, Grosbois V. 2012 Exploring causal pathways in demographic parameter variation: path analysis of mark-recapture data. *Methods Ecol Evol* **3**, 427–432. (doi:10.1111/j.2041-210X.2011.00150.x)

48. Zabala J, Lambin X, Soufflot J, Soufflot P, Chenesseau D, Millon A. 2020 Proximate causes and fitness consequences of double brooding in female barn owls. *Oecologia* **192**, 91–103. (doi:10.1007/s00442-019-04557-z)

49. Durant JM, Massemin S, Thouzeau C, Handrich Y. 2000 Body reserves and nutritional needs during laying preparation in barn owls. *Journal of Comparative Physiology B* **170**, 253–260. (doi:10.1007/s003600050283)

50. Chausson A, Henry I, Ducret B, Almasi B, Roulin A, Sergio F. 2014 Tawny Owl *Strix aluco* as an indicator of Barn Owl Tyto alba breeding biology and the effect of winter severity on Barn Owl reproduction. *Ibis* **156**, 433–441. (doi:10.1111/ibi.12148)

51. Roulin A. 2004 The function of food stores in bird nests: Observations and experiments in the Barn Owl Tyto alba. *Ardea* **92**, 69–78.

52. Frey C, Sonnay C, Dreiss A, Roulin A. 2010 Habitat, breeding performance, diet and individual age in Swiss Barn Owls (Tyto alba). *J Ornithol* **152**, 279–290. (doi:10.1007/s10336-010-0579-8)

53. Béziers P, Roulin A. 2016 Double brooding and offspring desertion in the barn owl Tyto alba. *J Avian Biol* **47**, 235–244. (doi:10.1111/jav.00800)

54. Taylor IR. 1994 *Barn owls*. 1st edn. Cambridge: Cambridge University Press.

55. Romero LM, Reed JM. 2005 Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comp Biochem Physiol A Mol Integr Physiol* **140**, 73–79. (doi:10.1016/J.CBPB.2004.11.004)

56. Almasi B, Roulin A, Jenni L. 2013 Corticosterone shifts reproductive behaviour towards self-maintenance in the barn owl and is linked to melanin-based coloration in females. *Horm Behav* **64**, 161–171. (doi:10.1016/j.yhbeh.2013.03.001)

57. Apolloni N, Grüebler MU, Arlettaz R, Gottschalk TK, Naef-Daenzer B. 2017 Habitat selection and range use of little owls in relation to habitat patterns at three spatial scales. *Anim Conserv* **65**, 210. (doi:10.1111/acv.12361)

58. Glennon MJ, Porter WF, Demers CL. 2002 An alternative field technique for estimating diversity of small-mammal populations. *J Mammal* **83**, 734–742. (doi:10.1644/1545-1542(2002)083<0734:AAFTFE>2.0.CO;2)

59. Todd IA, Tew TE, Macdonald DW. 2000 Arable habitat use by wood mice (*Apodemus sylvaticus*). 1. Macrohabitat. *J Zool* **250**, 299–303. (doi:10.1111/j.1469-7998.2000.tb00773.x)

60. Jareño D, Viñuela J, Luque-Larena JJ, Arroyo L, Arroyo B, Mougeot F. 2014 A comparison of methods for estimating common vole (*Microtus arvalis*) abundance in agricultural habitats. *Ecol Indic* **36**, 111–119. (doi:10.1016/J.ECOLIND.2013.07.019)

61. Fay R, Michler S, Laesser J, Jeanmonod J, Schaub M. 2020 Large-Scale Vole Population Synchrony in Central Europe Revealed by Kestrel Breeding Performance. *Front Ecol Evol* **7**, 512. (doi:10.3389/FEVO.2019.00512)

62. Séchaud R, Schalcher K, Almasi B, Bühler R, Safi K, Romano A, Roulin A. 2022 Home range size and habitat quality affect breeding success but not parental investment in barn owl males. *Sci Rep* **12**. (doi:10.1038/s41598-022-10324-7)

63. Labocha MK, Hayes JP. 2012 Morphometric indices of body condition in birds: A review. *J Ornithol* **153**, 1–22. (doi:10.1007/S10336-011-0706-1)

64. Sedinger JS, Lindberg MS, Riecke T V, Leach AG, Meixell BW, Nicolai CA, Koons DN. 2022 Do hunters target auxiliary markers? An example using black brant. *J Wildl Manage* **86**, e22172. (doi:10.1002/jwmg.22172)

65. Burnham KP. 1993 A theory for combined analysis of ring recovery and recapture data. In *Marked individuals in the study of bird populations.* (eds J-D Lebeton, PM North), pp. 199–213. Basel, Switzerland: Birkhauser Verlag.

66. Plummer M. 2003 JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd international workshop on distributed statistical computing*, pp. 1–10. Vienna, Austria.

67. Kellner K. 2021 jagsUI: A Wrapper Around 'rjags' to Streamline 'JAGS' Analyses.

68. R Development Core Team. 2021 R: A language and environment for statistical computing.

69. Kery M, Schaub M. 2012 *Bayesian Population Analysis Using WinBUGS*. Elsevier Inc. (doi:10.1016/C2010-0-68368-4)

70. Deeming CD. 2002 *Avian Incubation: Behaviour, Environment, and Evolution*. Oxford, UK: Oxford University Press.

71. Hanssen SA, Hasselquist D, Folstad I, Erikstad KE. 2005 Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society B: Biological Sciences* **272**, 1039–1046. (doi:10.1098/RSPB.2005.3057)

72. Romano A, Liker A, Bazzi G, Ambrosini R, Møller AP, Rubolini D. 2022 Annual egg productivity predicts female-biased mortality in avian species. *Evolution (N Y)* **76**, 2553–2565. (doi:10.1111/EVO.14623)

73. Visser ME, Lessells CM. 2001 The costs of egg production and incubation in great tits (*Parus major*). *Proc R Soc Lond B Biol Sci* **268**, 1271–1277. (doi:10.1098/RSPB.2001.1661)

74. Durant JM, Gendner JP, Handrich Y. 2004 Should I brood or should I hunt: a female barn owl's dilemma. *Can J Zool* **82**. (doi:10.1139/Z04-078)

75. Henry I, Antoniazza S, Dubey S, Simon C, Waldvogel C, Burri R, Roulin A. 2013 Multiple Paternity in Polyandrous Barn Owls (*Tyto alba*). *PLoS One* **8**, e80112. (doi:10.1371/JOURNAL.PONE.0080112)

76. Hatchwell BJ, Fowlie MK, Ross DJ, Russell AF. 1999 Incubation Behavior of Long-Tailed Tits: Why Do Males Provision Incubating Females? *Condor* **101**, 681–686. (doi:10.2307/1370201)

77. Martin TE, Ghalambor CK. 1999 Males Feeding Females during Incubation. I. Required by Microclimate or Constrained by Nest Predation? *Am Nat* **153**, 131–139. (doi:10.1086/303153)

78. Olson CR, Vleck CM, Vleck D. 2006 Periodic Cooling of Bird Eggs Reduces Embryonic Growth Efficiency. *Physiological and Biochemical Zoology* **79**, 927–936. (doi:10.1086/506003)

79. White FN, Kinney JL. 1974 Avian incubation. *Science (1979)* **186**, 107–115. (doi:10.1126/science.186.4159.107)

80. Ball GF, Ketterson ED. 2007 Sex differences in the response to environmental cues regulating seasonal reproduction in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 231–246. (doi:10.1098/RSTB.2007.2137)

81. Clark CJ. 2012 The role of power versus energy in courtship: what is the 'energetic cost' of a courtship display? (doi:10.1016/j.anbehav.2012.04.012)

82. Verboven N, Verhulst S. 1996 Seasonal Variation in the Incidence of Double Broods: The Date Hypothesis Fits Better than the Quality Hypothesis. *J Anim Ecol* **65**, 264. (doi:10.2307/5873)

83. O'Brien EL, Dawson RD. 2013 Experimental dissociation of individual quality, food and timing of breeding effects on double-brooding in a migratory songbird. *Oecologia* **172**, 689–699. (doi:10.1007/S00442-012-2544-0)

84. Nagy LR, Holmes RT. 2005 Food limits annual fecundity of a migratory songbird: an experimental study. *Ecology* **86**, 675–681. (doi:10.1890/04-0155)

85. Chausson A, Henry I, Almasi B, Roulin A. 2014 Barn Owl (*Tyto alba*) breeding biology in relation to breeding season climate. *J Ornithol* **155**, 273–281. (doi:10.1007/s10336-013-1012-x)

86. Ouin A, Paillat G, Butet A, Burel F. 2000 Spatial dynamics of wood mouse (*Apodemus sylvaticus*) in an agricultural landscape under intensive use in the Mont Saint Michel Bay (France). *Agric Ecosyst Environ* **78**, 159–165. (doi:10.1016/S0167-8809(99)00119-X)

87. Lambin X, Bretagnolle V, Yoccoz NG. 2006 Vole population cycles in northern and southern Europe: Is there a need for different explanations for single pattern? *Journal of Animal Ecology* **75**, 340–349. (doi:10.1111/J.1365-2656.2006.01051.X)

88. Verboven N;, Tinbergen JM;, Verhulst S. 2001 Food, reproductive success and multiple breeding in the Great Tit *Parus major*. *Ardea* **89**, 387–406.

89. Norberg RA. 1981 Temporary Weight Decrease in Breeding Birds May Result in More Fledged Young. *Am Nat* **118**, 838–850. (doi:10.1086/283874)

90. Kulaszewicz I, Wojczulanis-Jakubas K, Jakubas D. 2017 Trade-offs between reproduction and self-maintenance (immune function and body mass) in a small seabird, the little auk. *J Avian Biol* **48**, 371–379. (doi:10.1111/JAV.01000)

91. Nicolai CA, Sedinger JS. 2012 Trade-offs between offspring fitness and future reproduction of adult female black brent. *Journal of Animal Ecology* **81**, 798–805. (doi:10.1111/J.1365-2656.2012.01953.X)

92. Lucas FS, Moureau B, Jourdie V, Heeb P. 2005 Brood size modifications affect plumage bacterial assemblages of European starlings. *Mol Ecol* **14**, 639–646. (doi:10.1111/J.1365-294X.2005.02436.X)

93. Lack D. 1947 The Significance of Clutch-size. *Ibis* **89**, 302–352. (doi:10.1111/J.1474-919X.1947.TB04155.X)

94. Johnson M, Walters JR. 2008 Effects of Mate and Site Fidelity on Nest Survival of Western Sandpipers (*Calidris Mauri*). *Auk* **125**, 76–86. (doi:10.1525/AUK.2008.125.1.76)

95. Martin K. 1995 Patterns and Mechanisms for Age-dependent Reproduction and Survival in Birds. *Integr Comp Biol* **35**, 340–348. (doi:10.1093/ICB/35.4.340)

96. Pärt T. 1994 Male philopatry confers a mating advantage in the migratory collared flycatcher, *Ficedula albicollis*. *Anim Behav* **48**, 401–409. (doi:10.1006/ANBE.1994.1254)

97. Fawcett TW, Bleay C. 2009 Previous experiences shape adaptive mate preferences. *Behavioral Ecology* **20**, 68–78. (doi:10.1093/BEHECO/ARN116)

98. Pyle P, Spear LB, Sydeman WJ, Ainley DG. 1991 The Effects of Experience and Age on the Breeding Performance of Western Gulls. *Auk* **108**, 25–33. (doi:10.1093/AUK/108.1.25)

99. Altwegg R, Roulin A, Kestenholz M, L. J. 2003 Variation and covariation in survival, dispersal, and population size in barn owls. *Journal of Animal Ecology* , 391–399.

100. Kupán K, Székely T, Cruz-López M, Seymour K, Küpper C. 2021 Offspring desertion with care? Chick mortality and plastic female desertion in Snowy Plovers. *Behavioral Ecology* **32**, 428–439. (doi:10.1093/BEHECO/ARAA141)

101. Pilastro A, Biddau L, Marin G, Mingozzi T. 2001 Female Brood Desertion Increases with Number of Available Mates in the Rock Sparrow. *J Avian Biol* **32**, 68–72.

102. Goodburn SF. 1991 Territory quality or bird quality? Factors determining breeding success in the Magpie *Pica pica*. *Ibis* **133**, 85–90. (doi:10.1111/J.1474-919X.1991.TB04815.X)

103. Eldegard K, Sonerud GA. 2009 Female offspring desertion and male-only care increase with natural and experimental increase in food abundance. *Proceedings of the Royal Society B: Biological Sciences* **276**, 1713–1721. (doi:10.1098/RSPB.2008.1775)

104. Barbraud C, Weimerskirch H. 2005 Environmental conditions and breeding experience affect costs of reproduction in Blue Petrels. *Ecology* **86**, 682–692. (doi:10.1890/04-0075)

105. Meunier J, Pinto SF, Burri R, Roulin A. 2011 Eumelanin-based coloration and fitness parameters in birds: A meta-analysis. *Behav Ecol Sociobiol* **65**, 559–567. (doi:10.1007/S00265-010-1092-Z)

106. Roulin A, Almasi B, Meichtry-Stier KS, Jenni L. 2011 Eumelanin- and pheomelanin-based colour advertise resistance to oxidative stress in opposite ways. *J Evol Biol* **24**, 2241–2247. (doi:10.1111/j.1420-9101.2011.02353.x)

107. Almasi B, Jenni L, Jenni-Eiermann S, Roulin A. 2010 Regulation of stress response is heritable and functionally linked to melanin-based coloration. *J Evol Biol* **23**, 987–996. (doi:10.1111/j.1420-9101.2010.01969.x)

Supplementary material chapter 3:

S1: Covariates

Experience

Individuals were assigned to two different groups: first-time breeders and experienced adults (i.e., individuals with at least one previous breeding attempt), with value 1 for experienced and 0 for inexperienced birds. This information was based on the actual age, or the moult-dependent age determination of the individual described in the methods part of the manuscript and was therefore available for all individuals.

Laying date of first brood

Laying date was included as the day of the year when the first egg of the first brood was laid. Small numbers therefore indicate early laying, and higher numbers late laying. Missing laying dates were estimated using a normal distribution given the annual population mean and standard deviation.

Body condition index

Body condition index (BCI) was estimated for two different timepoints, during incubation and during brood-rearing period. We fitted a linear regression for each of the two timepoints using weight as the response and wing length, time of the day of capture and sex as explanatory variables. The residuals of the linear regressions were then used as a proxy for body condition, allowing us to correct for individual body size [69]. If multiple measurements were taken per individual and period, the mean of the calculated BCI was used. Missing BCI values were estimated using a normal distribution with sex- and year-specific population means and standard deviations.

Prey activity density

Prey activity density was calculated for five timepoints: pre-laying, during incubation, during brood-rearing and early as well as late winter. The laying date of the first egg (start of incubation) was used as basis to calculate the other timepoints. Pre-laying was defined as the timepoint 30 days before laying and nestling timepoint when the oldest nestling had a theoretical age of 30 days (mean age between hatching and fledging). Winter was divided into early winter (November-December) and late winter (January-February). For each 1.5 km buffer around the breeding nest box, the area covered by each of the 4 habitat types was extracted: Crop-rotation, grassland, biodiversity structures and border structures. The surface of each habitat category was multiplied with the corresponding activity density for small mammals and voles separately and then summed up to obtain the total activity density per nest box buffer area. Missing activity densities were estimated using a normal distribution with year-specific means and standard deviation.

Baseline and stress-induced corticosterone

Since corticosterone concentration per individual and reproductive period was sometimes measured repeatedly, a mean value for baseline and stress-induced concentration was used for the yearly value. Because an individual's stress profile is expected to be more closely related to previous measurements than to the population mean, missing values were estimated auto-regressively using a normal distribution with individual-specific means and a year-specific standard deviation. If no measurements were available for an individual, the sex-specific mean was used.

Eumelanin plumage spot diameter

If more than one measurement per individual and year was available, the mean of the measurements was taken. Missing values were estimated using a normal distribution with individual specific mean (value from previous year) and a sex specific standard deviation. If no measurements were available for an individual, sex specific mean was used.

Number of eggs, nestlings, and fledglings

The number of eggs, nestlings and fledglings was summed up for each adult and each year (Supp. mat. S 3). Depending on the year, the proportion of individuals performing a second brood varied between 6 up to 21%. Of these individuals who performed a second brood around 69% where females and 31% males. When measures of reproductive investment and success were not directly observed, they were estimated as a function of the previously described extrinsic and intrinsic covariates.

S2: Mathematical equations of the hierarchical model

$n^E: number\ of\ eggs$

$n^N: number\ of\ nestlings$

$n^F: number\ of\ fledglings$

$p^E: hatching\ success$

$p^F: fledging\ success$

$z: latent\ state$

$\varphi: survival\ probability$

$p: recapture\ probability$

$r: recovery\ probability$

$$n^E{}_{(i,t)} \sim Poisson(\psi_{(i,t)})$$

$$\begin{aligned}\log(\psi_{(i,t)}) = \alpha_{(sex)} &+ \beta_{1\,(sex)} * adult\ experience_{1(i,t)} \\ &+ \beta_{2\,(sex)} * laying\ date_{(i,t)} \\ &+ \beta_{3\,(sex)} * vole\ activity\ density\ pre-laying_{(i,t)} \\ &+ \beta_{4\,(sex)} * small\ mammal\ activity\ density\ pre-laying_{(i,t)}\end{aligned}$$

$$n^N{}_{(i,t)} \sim binomial(n^E{}_{(i,t)}, \rho^E{}_{(i,t)})$$

$$\begin{aligned}logit(\rho^E{}_{(i,t)}) = \alpha_{(sex)} &+ \beta_{1\,(sex)} * adult\ experience_{(i,t)} \\ &+ \beta_{2\,(sex)} * clutch\ size_{(i,t)} \\ &+ \beta_{3\,(sex)} * laying\ date_{(i,t)} \\ &+ \beta_{4\,(sex)} * adult\ body\ condition\ incubation_{(i,t)} \\ &+ \beta_{5\,(sex)} * vole\ activity\ density\ incubation\ _{(i,t)} \\ &+ \beta_{6\,(sex)} * small\ mammal\ activity\ density\ incubation\ _{(i,t)}\end{aligned}$$

$$n^F{}_{(i,t)} \sim binomial(n^N{}_{(i,t)}, \rho^N{}_{(i,t)})$$

$$\begin{aligned} logit\left(\rho^N{}_{(i,t)}\right) = {} & \alpha_{(sex)} + \beta_{1\,(sex)} * adult\ experience_{(i,t)} \\ & + \beta_{2\,(sex)} * number\ of\ nestlings_{(i,t)} \\ & + \beta_{3\,(sex)} * laying\ date_{(i,t)} \\ & + \beta_{4\,(sex)} * adult\ body\ condition\ brood\ rearing_{(i,t)} \\ & + \beta_{5\,(sex)} * vole\ activity\ density\ brood\ rearing_{\,(i,t)} \\ & + \beta_{6\,(sex)} * small\ mammal\ activity\ density\ brood\ rearing_{\,(i,t)} \end{aligned}$$

$$z_{(i,t)} \sim Bernoulli(z_{(i,t-1)} * \varphi_{(i,t-1)})$$

$$alive_{(i,t)} \sim Bernoulli(z_{(i,t)} *\ p_{(VHF_{(i,t-1)}, sex_{(i)})})$$

$$dead_{(i,t)} \sim Bernoulli((z_{(i,t-1)} - z_{(i,t)}) * r_{(VHF_{(i,t-1)}, sex_{(i)})})$$

$$\begin{aligned} logit(\varphi_{(i,t-1)} = {} & \alpha_{(sex)} + \beta_{1\,(sex)} * adult\ experience_{1(i,t-1)} \\ & + \beta_{2\,(sex)} * adult\ body\ condition\ brood\ rearing_{(i,t-1)} \\ & + \beta_{3\,(sex)} * number\ of\ nestlings_{(i,t-1)} \\ & + \beta_{4\,(sex)} * number\ of\ fledglings_{(i,t-1)} \\ & + \beta_{5\,(sex)} * baseline\ corticosterone_{(i,t-1)} \\ & + \beta_{6\,(sex)} * response\ corticosterone_{(i,t-1)} \\ & + \beta_{7\,(sex)} * plumage\ spot\ diameter_{(i,t-1)} \\ & + \beta_{8\,(sex)} * vole\ activity\ density\ incubation_{(i,t-1)} \\ & + \beta_{9\,(sex)} * small\ mammal\ activity\ density\ incubation_{(i,t-1)} \\ & + \beta_{10\,(sex)} * vole\ activity\ density\ winter_{(i,t-1)} \\ & + \beta_{11\,(sex)} * small\ mammal\ activity\ density\ winter_{(i,t-1)} \end{aligned}$$

S3: Table reproduction

Table S3: Number of breeding birds per year which performed minimum one (1st brood) or two (2nd brood) broods. Number of eggs (E), number of nestlings (N) and fledglings (F) and the corresponding hatching (HS) and fledging success (FS) with the corresponding standard deviation are given for each year and for first and second brood. The last two columns give information on the number and proportion of birds performing a second brood for male (m) and female (m) with given experience (0 = naive; 1 = experienced).

Year	1st brood			2nd brood				
	Number of. breeding birds	Number of eggs, nestlings, fledglings	Hatching success, fledging success	Number of breeding birds	Number of eggs, nestlings, fledglings	Hatching success, fledging success	Sex	Experience
2017	244	E: 6.8 ± 1.6 N: 5.2 ± 2.1 F: 3.2 ± 2.1	HS: 0.8 ± 0.3 FS: 0.6 ± 0.3	47 (19%)	E: 6.9 ± 1.8 N: 4.8 ± 2.2 F: 3.8 ± 1.6	HS: 0.7 ± 0.3 FS: 0.8 ± 0.2	f: 32 (24%)	0: 17 (53%) 1+: 15 (47%)
							m: 15 (14%)	0: 9 (60%) 1+: 6 (40%)
2018	125	E: 5.6 ± 1.1 N: 4.0 ± 2.0 F: 2.9 ± 1.7	HS: 0.7 ± 0.3 FS: 0.7 ± 0.3	7 (6%)	E: 7.1 ± 1.9 N: 6.0 ± 1.2 F: 4.3 ± 2.4	HS: 0.8 ± 0.1 FS: 0.7 ± 0.3	f: 6 (9%)	0: 2 (33%) 1+: 4 (67%)
							m: 1 (2%)	0: 1 (100%) 1+: 0 (0%)
2019	134	E: 6.2 ± 1.3 N: 4.4 ± 1.9 F: 2.5 ± 1.6	HS: 0.7 ± 0.3 FS: 0.6 ± 0.3	28 (21%)	E: 7.2 ± 2.5 N: 5.0 ± 1.8 F: 3.1 ± 1.2	HS: 0.7 ± 0.2 FS: 0.7 ± 0.2	f: 20 (30%)	0: 4 (20%) 1+: 16 (80%)
							m: 8 (12%)	0: 1 (13%) 1+: 7 (87%)
2020	212	E: 5.9 ± 1.3 N: 4.5 ± 2.0 F: 2.9 ± 1.8	HS: 0.8 ± 0.3 FS: 0.7 ± 0.3	34 (20%)	E: 8.0 ± 3.5 N: 4.8 ± 2.3 F: 3.3 ± 1.7	HS: 0.6 ± 0.2 FS: 0.7 ± 0.2	f: 25 (23%)	0: 5 (20%) 1+: 20 (80%)
							m: 18 (18%)	0: 5 (28%) 1+: 13 (72%)

S4: Dead recovery (r) and recapture probability (p)

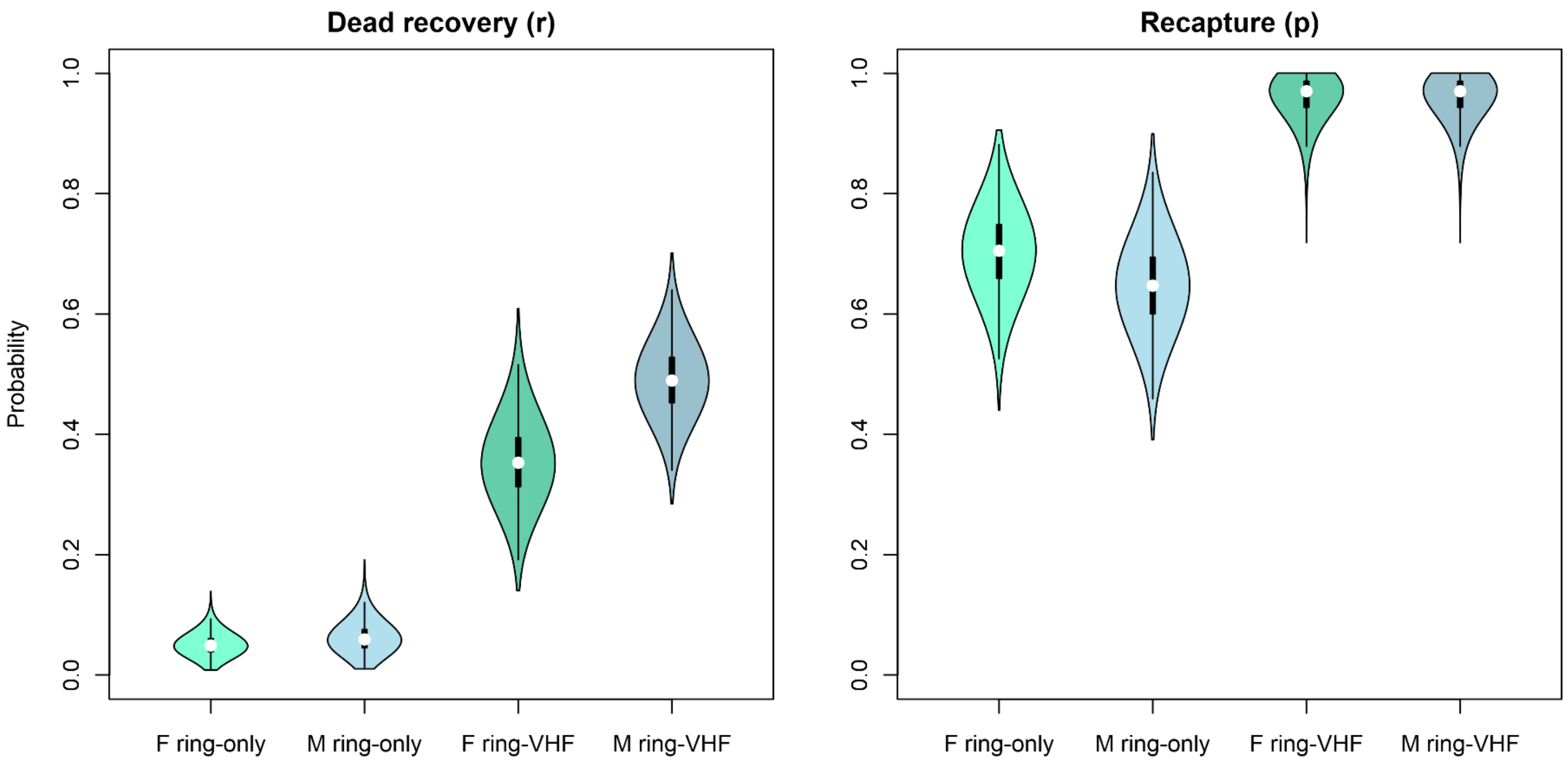


Figure S4: Mean (white point) and posterior distribution of estimates of dead recovery probability (r, left) and recapture probability (p, right) for the two sexes (females: green, males: blue) and the marking method (ring-only: light green/blue, ring-VHF: dark green/blue).

S5: Survival probability (φ)

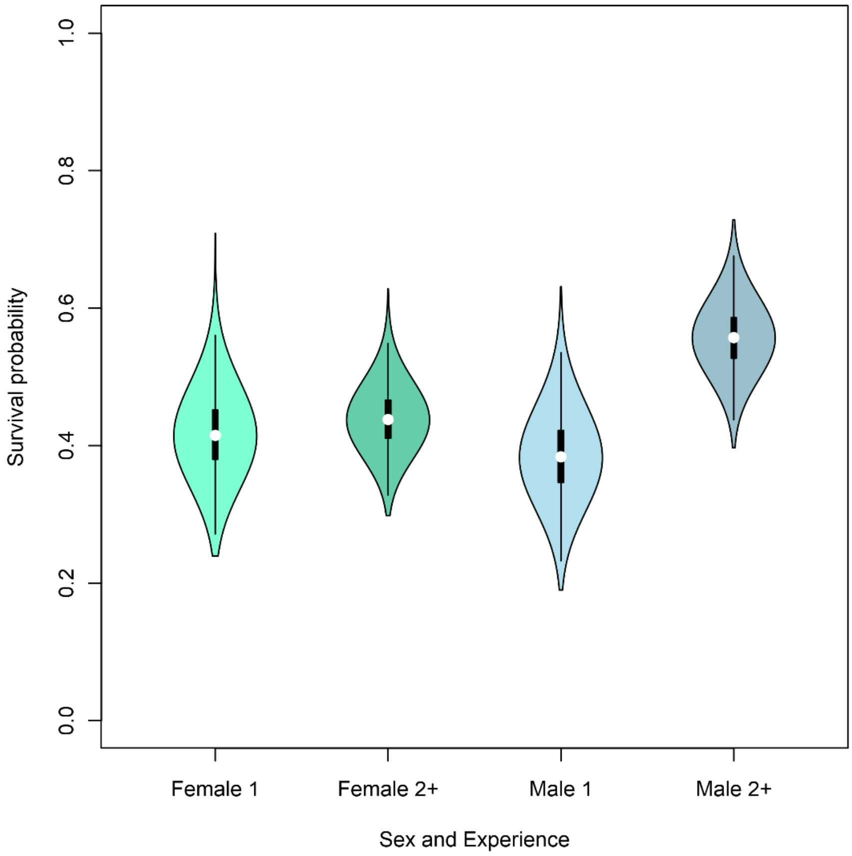


Figure S5: Mean (white point) and posterior distribution of estimates of survival probability for the two sexes (females: green, males: blue) and experience (inexperienced: light green/blue, experienced: dark green/blue.

S6: Table number of eggs

Table S6: Mean, lower and upper 95% credible interval (CrI) and f (the proportion of the posterior with the same sign as the mean), for the estimates of the regression parameters (ß) on annual number of eggs produced. Models are based on 556 individuals and 5 years.

Number of eggs	**ß mean (95% CrI)**	**f**
Female		
Intercept: Unexperienced (0)	**2.00 (1.94, 2.06)**	**1.000**
Experienced (1)	**0.06 (−0.02, 0.13)**	**0.930**
Laying date first clutch	**−0.24 (−0.29, −0.18)**	**1.000**
small mammal activity density, pre-laying	**0.09 (0.04, 0.14)**	**1.000**
vole activity density, pre-laying	**−0.04 (−0.09, 0.00)**	**0.978**
Male		
Intercept: Unexperienced (0)	**2.01 (1.94, 2.07)**	**1.000**
Experienced (1)	**−0.06 (−0.14, 0.02)**	**0.939**
Laying date	**−0.10 (−0.16, −0.05)**	**1.000**
Small mammal activity density, pre-laying	**0.06 (0.00, 0.12)**	**0.981**
Vole activity density, pre-laying	−0.02 (−0.07, 0.03)	0.805

S7: Table hatching success

Table S7: Mean, lower and upper 95% credible interval (CrI) and f (the proportion of the posterior distribution on the same side of 0 as the mean), for the estimates of the regression parameters (ß) on hatching success. Models are based on 556 individuals and 5 years.

Hatching success	**ß mean (95% CrI)**	**f**
Female		
Intercept: Unexperienced (0)	**0.95 (0.81, 1.08)**	**1.000**
Experienced (1)	**0.15 (−0.02, 0.32)**	**0.959**
Number of eggs	**−0.48 (−0.55, −0.41)**	**1.000**
Laying date	**−0.39 (−0.53, −0.26)**	**1.000**
Body condition index, incubation	**0.23 (0.13, 0.32)**	**1.000**
Small mammal activity density, incubation	0.04 (−0.09, 0.17)	0.721
Vole activity density, incubation	**0.22 (0.12, 0.32)**	**1.000**
Male		
Intercept: Unexperienced (0)	**1.13 (0.98, 1.29)**	**1.000**
Experienced (1)	**0.18 (−0.02, 0.38)**	**0.962**
Number of eggs	**−0.32 (−0.41, −0.23)**	**1.000**
Laying date	−0.01 (−0.16, 0.13)	0.574
Body condition index, incubation	**0.35 (0.12, 0.53)**	**0.997**
Small mammal activity density, incubation	0.04 (−0.09, 0.18)	0.729
Vole activity density, incubation	**0.09 (−0.05, 0.17)**	**0.930**

S8: Table fledging success

Table S8: Mean, lower and upper 95% credible interval (CrI) and f (the proportion of the posterior distribution on the same side of 0 as the mean), for the estimates of the regression parameters (ß) on fledging success. Models are based on 556 individuals and 5 years.

Fledging success	**ß mean (95% CrI)**	**f**
Female		
Intercept: Unexperienced (0)	**0.57 (0.42, 0.72)**	**1.000**
Experienced (1)	0.05 (–0.14, 0.24)	0.699
Number of nestlings	**–0.20 (–0.30, –0.11)**	**1.000**
Laying date	0.01 (–0.10, 0.12)	0.553
Body condition index, brood-rearing	**0.10 (–0.01, 0.20)**	**0.964**
Small mammal activity density, brood-rearing	0.02 (–0.09, 0.14)	0.639
Vole activity density, brood-rearing	–0.02 (–0.12, 0.09)	0.640
Male		
Intercept: Unexperienced (0)	**0.71 (0.55, 0.88)**	**1.000**
Experienced (1)	–0.03 (–0.23, 0.18)	0.599
Number of nestlings	**–0.20 (–0.31, –0.10)**	**1.000**
Laying date	–0.05 (–0.15, 0.05)	0.833
Body condition index, brood-rearing	**–0.15 (–0.35, 0.06)**	**0.920**
Small mammal activity density, brood-rearing	–0.02 (–0.13, 0.09)	0.646
Vole activity density, brood-rearing	0.06 (–0.05, 0.17)	0.860

S9: Table survival-, recovery-, recapture probability

Table S9: Mean, lower and upper 95% credible interval (CrI) and f (the proportion of the posterior distribution on the same side of 0 as the mean), for the estimates of the regression parameters (ß) on adult survival. Mean, lower and upper 95% credible interval (CrI) for estimated dead recovery and recapture probability. Models are based on 556 individuals and 5 years.

Survival probability	**ß mean (95% CrI)**	**f**
Female		
Intercept: Unexperienced (0)	**−0.34 (−0.76, 0.11)**	**0.935**
Experienced (1)	0.09 (−0.44, 0.61)	0.640
Body condition index, brood-rearing	−0.05 (−0.28, 0.18)	0.655
Number of nestlings	−0.17 (−0.49, 0.15)	0.850
Number of fledglings	**0.44 (0.11, 0.79)**	**0.996**
Baseline GC	**−0.20 (−0.46, 0.04)**	**0.943**
Stress-induced GC	0.14 (−0.11, 0.40)	0.865
Average diameter plumage spots	**0.25 (0.01, 0.50)**	**0.979**
Small mammal activity density, incubation	**0.28 (−0.02, 0.60)**	**0.968**
Vole activity density, incubation	−0.00 (−0.31, 0.30)	0.514
Small mammal activity density, early winter	0.01 (−0.27, 0.30)	0.538
Vole activity density, early winter	−0.10 (−0.41, 0.19)	0.759
Male		
Intercept: Unexperienced (0)	**−0.47 (−0.94, 0.00)**	**0.975**
Experienced (1)	**0.71 (0.15, 1.26)**	**0.993**
Body condition index, brood-rearing	0.04 (−0.42, 0.50)	0.564
Number of nestlings	**−0.32 (−0.73, 0.08)**	**0.941**
Number of fledglings	0.21 (−0.17, 0.60)	0.863
Baseline GC	0.13 (−0.14, 0.41)	0.832
Stress-induced GC	−0.15 (−0.41, 0.10)	0.879
Average diameter plumage spots	**0.31 (0.04, 0.60)**	**0.987**
Small mammal activity density, incubation	−0.15 (−0.44, 0.12)	0.866
Vole activity density, incubation	**−0.43 (−0.76, −0.09)**	**0.993**
Small mammal activity density, early winter	−0.12 (−0.41, 0.17)	0.789
Vole activity density, early winter	**0.50 (0.17, 0.87)**	**0.999**
Dead recovery probability		
Male ring-only	0.06 (0.03, 0.12)	
Male ring-VHF	0.49 (0.38, 0.60)	
Female ring-only	0.05 (0.02, 0.09)	
Female ring-VHF	0.36 (0.24, 0.48)	
Recapture probability		
Male ring-only	0.65 (0.51, 0.78)	
Male ring-VHF	0.96 (0.87, 1.00)	
Female ring-only	0.70 (0.57, 0.82)	
Female ring-VHF	0.93 (0.80, 1.00)	

General Discussion

In environments with distinct seasons, the availability of resources undergoes significant fluctuations. These fluctuations result in varying food supplies, particularly during the colder non-breeding season. Consequently, there may be changes in the distribution and abundance of prey between the breeding and non-breeding seasons, leading to different habitat preferences. Habitat selection, a fundamental concept in ecology [9,16], deserves therefore equal attention during and outside of the breeding season, particularly for species facing elevated mortality risks during non-breeding periods [29]. Natural selection favours individuals capable of exploiting abundant and high-quality resources, leading to positive effects on their energy expenditure, breeding success, and survival chances. I was therefore especially interested in how changes in prey availability affect animal behaviour and fitness during a demanding period within the annual life cycle. By using the barn owl as study species and an exceptional dataset, my research has unveiled novel insights into the non-breeding period of resident animals. Due to year-round information on prey availability, I was able to discuss how changes in food availability over large temporal and spatial scales can affect an animal's habitat choice, activity patterns as well as survival and reproduction. By investigating the rather under-investigated non-breeding period, I contributed to bridge the knowledge gap between the breeding and the non-breeding period, to work towards an understanding of the full annual cycle of the study species [1].

Habitat selection in dynamic, human-influenced landscapes

Synanthropic species, that have co-evolved with human-altered habitats, need to adapt to habitat changes occurring within this anthropogenically influenced system [68]. While certain bird species demonstrate significant potential for adapting to human-made habitats [69,70], the current rapid pace of changes often restricts the time available for birds to adapt towards the changes [71]. Comprehending the degree of an animals' reliance on resources in human-dominated landscapes and their adaptability to adapt towards anthropogenic changes in resource availability is most important in understanding the ecology of synanthropic species [72]. The acquired knowledge may help us us to proactively anticipate and tackle potential threats that may arise or have already emerged due to human activities. By collecting year-round data on small mammal availability, we gained insights into how agricultural dynamics influenced the distribution of food resources of the barn owl. This allowed us to understand how these changes in resource distribution influenced habitat preferences of the study species between the breeding and the non-breeding period.

While studies conducted during the breeding period have shown the ability of barn owls to utilize various habitat types for hunting within agricultural landscapes [73], my study showed that, in addition to semi-natural habitats, grasslands serve as less disturbed habitats for small mammals, especially after harvest [63–67]. These shifts in prey availability from large parts of the cultivated area into grasslands and semi natural habitats then led to a grassland-oriented habitat selection during the non-breeding period. The seasonal disruptions caused by harvesting activities show the potential to alter predator-prey dynamics, creating pressures that can affect habitat use. While I provided insight into habitat selection during the non-breeding period, the impact of harvesting on habitat selection during the breeding period remains unclear at present. Take, for instance, early and late breeders: the harvesting process might occur during different stages of the brood, potentially impacting reproductive success in distinct ways for each stage. Furthermore habitat selection alterations aren't necessarily limited to long term seasonal shifts; they could also occur within shorter time periods. For instance, the changes in vegetation height within certain agricultural plantations (e.g. start of vegetation period, frequent mowing of grassland) could impact barn owls' hunting abilities within relatively short time intervals. Dense and tall growing, long-lasting plantations such as rape, maize or cereals might become less suitable hunting grounds for barn owls once they reached a certain growth stage. This could occur because areas covered with dense vegetation tend to limit prey accessibility for birds of prey [74,75]. Exploring the habitat use of barn owls on a finer temporal resolution during both, breeding and non-breeding period, especially in relation to shifting habitat features, would be particularly compelling.

Moreover, the gathered data presents an opportunity to explore individual-specific habitat preferences, such as based on sex or plumage coloration. Initial analyses suggest potential differences in habitat selection between sexes: preliminary findings hint at stronger grassland preferences and crop rotation avoidance among males, while females appear to utilize crop rotation based on its availability. This suggests that sexes might respond differently to shifts in agricultural practices, which may be relevant for conservation measures.

Throughout my study, I not only demonstrated shifts in barn owl habitat selection but also revealed noteworthy variations in vole and small mammal activity density between the breeding and non-breeding period. I found that changes in vole and small mammal activity density is significantly influenced by the type of habitat they inhabit. The findings from this research therefore have broader implications beyond just barn owls, as they may offer new insights into the ecology of small mammals themselves or other small mammal-hunting birds of prey. The data we've gathered during the study period offers an opportunity to explore the ecology of small mammals within the agricultural landscape, apart from focusing on the barn owl. In conclusion, the discoveries made during this study hold relevance for a wider ecological context, making them pertinent and intriguing for researchers interested in the interactions between birds of prey, small mammals, and their habitats.

The effects of environmental conditions on activity patterns

The ability to exploit profitable resources in a fast-changing environment can lead to fitness advantages in terms of survival and reproduction [9]. For example, using a certain habitat type with a high availability of resources may result in energetic advantages, that are particularly important in times when animals are under high selective pressure. In temperate regions, the non-breeding period is characterized by dropping temperatures which restrict the availability of resources but also increase the energy expenditure for thermoregulation [19–22,76]. These selective pressures can considerably affect population dynamics [76,77], making it especially important to unveil the energetic consequences of environmental conditions on individuals and populations.

In my research, I found that the overall activity patterns during the breeding period, as measured by VeDBA (Vectorial Dynamic Body Acceleration), show considerable variations based on environmental conditions. Specifically, during adverse weather conditions, the owls exhibit reduced overall activity, indicating a tendency to minimize energy expenditure during periods with suboptimal conditions. When faced with challenges like wind and rain causing movement and noise, birds of prey can have difficulty spotting their prey using visual or acoustic cues [78–82]. These very conditions might be advantageous for their prey's activities and indeed rain and wind has been shown to correlate with in small mammal activity [78,83], as these conditions provide a certain level of protection from predation. Small mammals also exhibit the ability to adjust their activity patterns based on temperature variations, particularly in winter [84–86].

This adaptive behaviour may result in changes in their accessibility to predators, as their activity shifts in relation to the predator's own activity periods. Weather conditions are therefore able to disrupt or enhance predator prey interactions. Identifying how environmental conditions affect predator and prey is therefore key to understand how modified predator prey relationships affect predator populations.

I presented findings suggesting that barn owls adjust their nocturnal activity to coincide with peak prey activity. If this holds true and considering that small mammals alter their activity patterns between summer and winter [84–86], the nightly activity pattern could be considerably different during the breeding season. Such differences could emerge trough a change in prey activity as well as the need for increased number of prey items to feed the chicks. Comparing data collected during the breeding period with those collected during the non-breeding period could help to unveil how strongly barn owl activity is related to the activity of their prey.

While the shown effects of meteorological conditions on activity pattern may not be entirely unexpected, they may provide greater significance in the context of climate change. Anthropogenic climate change led to fast changes in climatic conditions and many biological responses have shown to be driven by changes in conditions during both, the breeding and the non-breeding period [76]. As climate change progresses, the implications of these observed behavioural adaptations may become more noteworthy. For short eared owls for example, extreme meteorological conditions like high windspeed or increased sunshine have shown to affect the reproductive success, most probably due to increased cost for thermoregulation and lower hunting success [79]. As extreme weather events, such as heat waves, heavy precipitation and extreme winds are predicted to become more frequent under climate change [87,88], it may be important to investigate how the fitness of animals is affected by such events and whether or how animals adapt to cope with such changing conditions. While barn owls may profit from certain climatic changes in winter, such as higher temperatures, other predicted aspects of climate change during winter, such as increased winter precipitation or extreme winds [87] may negatively affect winter survival and upcoming reproduction. Personal observations during the study period suggest that breeding seasons could be impacted by cold, precipitation-heavy springs, and dry, hot summers. However, further testing is needed to confirm these potential effects on reproduction. I strongly believe that studying how barn owls but also their prey respond to climatic changes within the whole annual cycle could aid in anticipating potential shifts in the selective pressure of weather conditions on barn owl population dynamics.

In my thesis I also showed that individual plumage coloration is linked with activity patterns when exposed to certain environmental conditions. These findings imply the presence of individual-specific habitat and prey preferences [89,90] during the non-breeding period. Such individual-specific differences would result in distinct responses to changes of prey availability within different habitat types, ultimately impact survival but also upcoming reproduction [91]. Barn owls for example show a distinct preference for certain prey which is associated with pheomelanic plumage coloration [90,92]. When structures which support a particular prey species, decrease, or disappear, this may lead to a disproportionate selection of individuals with a specific plumage coloration. As plumage coloration is to a certain degree associated with sex [92] the effects may change sex-specific survival probabilities, leading to a shift in the sex ratio with the following consequences for population viability [93]. Using high resolution movement data collected within a test study during the non-breeding period, I will be able to further investigate how individuals may adapt their behaviour to environmental conditions, such as food availability or habitat type. Furthermore the collection of high-resolution data during the breeding period [94] allows to investigate if individual specific activity patterns differ between seasons.

Selective pressure of individual and environmental conditions on animals' fitness

To better understand how individual and environmental factors affect survival and reproduction I dedicated my third chapter to this topic. Life history theory suggests that animals have to trade-off survival and reproduction to optimise their lifetime reproductive success and are therefore expected to trade off current reproduction with survival and success of future reproduction [23,95]. The decision on how much to invest in current reproduction is shaped by individual quality and environmental conditions [52,96–99]. In many studies exploring the impact of individual- and environmental factors on an organism's fitness, the focus is often narrowed down to either survival or reproduction and their respective relationships with environmental or individual conditions. However, this restricted approach may not fully unveil the wide range of potential effects. It is essential to recognize that environmental and individual conditions during various periods of an organism's life cycle can directly influence both reproduction and survival. Additionally, the effects of experienced conditions on reproductive traits can, in turn, affect survival through reproductive costs. To gain a comprehensive and interconnected understanding of annual survival, a wealth of data on environmental and individual factors spanning several years is necessary. Unfortunately, acquiring such an extensive dataset for wild species is often challenging and resource intensive.

In my study species, the barn owl, breeding early in the season and experiencing high food availability during reproduction were related to increased reproductive success. However, males and females reacted differently to increased reproductive investment. While female survival was positively associated with reproductive output, males experienced reproductive costs, leading to a decrease in annual survival after high reproductive investment. Male survival was linked to prey availability during winter following reproduction, indicating a possible compensatory mechanism effect, suggesting that males may react more sensitive to harsh winter conditions than females. Leading to the question whether prey availability during winter affects the oncoming reproduction, more specifically time of brood initiation and reproductive success. Given the presented results one may expect that male reproductive success may be more strongly dependent on wintering conditions than females. Indeed research on a migratory bird species showed that reproductive success for males, but not females, is influenced by the environmental conditions encountered during the non-breeding period [100]. I would therefore assume that males experiencing favourable conditions during winter may be capable of breeding earlier and show higher reproductive success than males inhabiting poor non-breeding habitat.

Conclusion

Investigating the non-breeding period provides information on how animals cope with the challenges of this understudied period and helps to understand the evolution of behaviour, life history trade-offs and the selective pressures which are currently acting on survival and reproduction. In my thesis I demonstrated that seasonal changes in anthropogenic landscape use led to fluctuations in food availability between the breeding and the non-breeding seasons, with the resulting consequences for habitat selection. Prey activity patterns, weather conditions as well as prey availability within different habitat types were related to barn owl activity patterns. I furthermore presented that female survival was positively related to reproductive output, while males experienced distinct reproductive costs. However, these costs might be mitigated in males which experience higher food availability during the non-breeding period. From the presented small mammal monitoring data, it can be inferred that the food supply during the non-breeding period is generally reduced and primarily concentrates on a few structures within the agricultural landscape. This implies that changes in agricultural practices can quickly lead to significant alterations in food availability for barn owls. While my research has provided initial insights into how agricultural practices can alter the availability and distribution of prey between breeding and non-breeding periods, the ramifications of abrupt changes during harvesting periods and their potential to disrupt predator-prey dynamics ask for further investigation. Furthermore, I presented sex-specific costs of reproduction and a link between male survival and food availability after reproduction. It would be interesting to explore in more detail how food availability during the non-breeding period affects the reproductive costs experienced by male barn owls in upcoming reproduction. While we were limited by the resolution of our data, fine-scaled movement data could reveal whether owls adapt their behaviour towards habitat or prey type and how adaptations in hunting behaviour might contribute to their survival and reproductive success.

My thesis has contributed to enhancing our understanding of the non-breeding ecology of barn owls, offering fresh perspectives and new ideas for further research on various dimensions of ecological research. By doing so I underlined the importance to investigate the non-breeding period to accomplish a year-round picture of barn owl ecology and other resident predators dealing with anthropogenically induced habitat variability. As we continue to navigate a rapidly evolving world, these findings underscore the importance of a holistic understanding of animal ecology to ensure the long-term survival of these species inhabiting dynamic landscapes.

Publication List

1. Séchaud R., Schalcher K., Almasi B., **Bühler R.,** Safi K., Romano A., Roulin A. (2022): Home range size and habitat quality affect breeding success but not parental investment in barn owl males, Scientific Reports 20, 12(1): 6516, https://doi.org/10.1038/s41598-022-10324-7

2. **Bühler R.,** Schalcher K., Séchaud R., Michler S., Apolloni N., Roulin A., Almasi B., (2023): Influence of prey availability on habitat selection during the non-breeding period in a resident bird of prey, Movement Ecology 11, 14 (2023), https://doi.org/10.1186/s40462-023-00376-3

References

1. Marra P, Cohen E, Loss S, Rutter J, Tonra C. 2015 A call for full annual cycle research in animal ecology. *Biol Lett* **11**. (doi:10.1098/rsbl.2015.0552)

2. Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. 2011 Carry-over effects as drivers of fitness differences in animals. *J Anim Ecol* **80**, 4–18. (doi:10.1111/j.1365-2656.2010.01740.x)

3. Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2004 Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society, Biological sciences* **271**, 59–64. (doi:10.1098/rspb.2003.2569)

4. Robb GN, McDonald RA, Chamberlain DE, Reynolds SJ, Harrison TJE, Bearhop S. 2008 Winter feeding of birds increases productivity in the subsequent breeding season. *Biol Lett* **4**, 220–223. (doi:10.1098/rsbl.2007.0622)

5. Saino N, Szep T, Romano M, Rubolini D, Spina F, Moller AP. 2004 Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* **7**, 21–25. (doi:10.1046/j.1461-0248.2003.00553.x)

6. Cook JG, Johnson BK, Cook RC, Riggs RA, Delcurto T, Bryant LD, Irwin LL. 2004 Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* **155**, 1–61. (doi:10.2193/0084-0173)

7. Gunnarsson TG, Gill JA, Newton J, Potts PM, Sutherland WJ. 2005 Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society, Biological sciences* **272**, 2319–2323. (doi:10.1098/rspb.2005.3214)

8. Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V, Hebblewhite M. 2015 The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology* **96**, 1741–1753. (doi:10.1890/14-1401.1)

9. Boyce MS, McDonald LL. 1999 Relating populations to habitats using resource selection functions. *Trends Ecol Evol* **14**, 268–272. (doi:10.1016/S0169-5347(99)01593-1)

10. Ellington EH, Muntz EM, Gehrt SD. 2020 Seasonal and daily shifts in behavior and resource selection: how a carnivore navigates costly landscapes. *Oecologia* **194**, 87–100. (doi:10.1007/s00442-020-04754-1)

11. Rice MB, Apa AD, Wiechman LA. 2017 The importance of seasonal resource selection when managing a threatened species: targeting conservation actions within critical habitat designations for the Gunnison sage-grouse. *Wildlife Research* **44**, 407–417. (doi:10.1071/WR17027)

12. Sperry JH, Weatherhead PJ. 2009 Does Prey Availability Determine Seasonal Patterns of Habitat Selection in Texas Ratsnakes. *J Herpetol* **43**, 55–64. (doi:10.1670/08-058R1.1)

13. Larter NC, Gates CC. 2011 Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. *Can J Zool* **69**, 2677–2685. (doi:10.1139/Z91-376)

14. Alatalo R V. 1981 Habitat selection of forest birds in the seasonal environment of Finland. *Ann Zool Fennici* **18**, 103–114.

15. Long RA, Kie JG, Terry Bowyer R, Hurley MA. 2009 Resource Selection and Movements by Female Mule Deer *Odocoileus hemionus*: Effects of Reproductive Stage. *Wildlife Biol* **15**, 288–298. (doi:10.2981/09-003)

16. Johnson DH. 1980 The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* **61**, 65–71. (doi:10.2307/1937156)

17. Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002 *Resource selection by animals*. 2. ed. Dordrecht: Kluwer Academic Publishers.

18. Stearns SC. 1992 *The Evolution of Life Histories*. Oxford, UK: Oxford University Press.

19. Biebach H. 1996 Energetics of Winter and Migratory Fattening. In *Avian Energetics and Nutritional Ecology*, pp. 280–323. Springer, Boston, MA. (doi:10.1007/978-1-4613-0425-8_9)

20. McCafferty DJ, Moncrieff JB, Taylor IR. 2001 How much energy do barn owls (*Tyto alba*) save by roosting? *J Therm Biol* **26**, 193–203. (doi:10.1016/S0306-4565(00)00042-5)

21. Norrdahl K, Klemola T, Korpimäki E. 2002 Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos* **99**, 419–430. (doi:10.1034/J.1600-0706.2002.12025.X)

22. Newton I. 1998 *Population limitation in birds*. Academic Press.

23. Williams GC. 1966 Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. *Am Nat* **100**, 687–690.

24. Bryant DM. 1979 Reproductive Costs in the House Martin (*Delichon urbica*). *Journal of Animal Ecology* **48**, 655–675. (doi:10.2307/4185)

25. Verhulst S. 1998 Multiple breeding in the Great Tit, II. The costs of rearing a second clutch. *Funct Ecol* **12**, 132–140. (doi:10.1046/J.1365-2435.1998.00165.X)

26. Nilsson JA, Svenssonn E. 1996 The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proc R Soc Lond B Biol Sci* **263**, 711–714. (doi:10.1098/RSPB.1996.0106)

27. Rivalan P, Prévot-Julliard AC, Choquet R, Pradel R, Jacquemin B, Girondot M. 2005 Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. *Oecologia* **145**, 564–574. (doi:10.1007/S00442-005-0159-4)

28. Siriwardena GM, Calbarde NA, Vickery JA. 2008 Farmland birds and late winter food: does seed supply fail to meet demand? *Ibis* **150**, 585–595. (doi:10.1111/j.1474-919X.2008.00828.x)

29. Altwegg R, Roulin A, Kestenholz M, Jenni L. 2006 Demographic effects of extreme winter weather in the barn owl. *Oecologia* **149**, 44–51. (doi:10.1007/s00442-006-0430-3)

30. Broggi J, Watson H, Nilsson J, Nilsson J-Å. 2022 Carry-over effects on reproduction in food-supplemented wintering great tits. *J Avian Biol* **2022**, e02969. (doi:10.1111/jav.02969)

31. Pyke GH, Pulliam HR, Charnov EL. 1977 Optimal Foraging. *Q Rev Biol* **52**, 137–154. (doi:10.1086/409852)

32. Pyke GH. 1984 Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics* **15**, 523–575. (doi:10.1146/ANNUREV.ES.15.110184.002515)

33. Nadjafzadeh M, Hofer H, Krone O. 2016 Sit-and-wait for large prey: Foraging strategy and prey choice of White-tailed Eagles. *J Ornithol* **157**, 165–178. (doi:10.1007/s10336-015-1264-8)

34. Gleiss AC, Wilson RP, Shepard ELC. 2011 Making overall dynamic body acceleration work. *Methods Ecol Evol* **2**, 23–33. (doi:10.1111/j.2041-210X.2010.00057.x)

35. Qasem L, Cardew A, Wilson A, Griffiths I, Halsey LG, Shepard ELC, Gleiss AC, Wilson R. 2012 Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS One* **7**, e31187. (doi:10.1371/journal.pone.0031187)

36. Hounslow JL, Brewster LR, Lear KO, Guttridge TL, Daly R, Whitney NM, Gleiss AC. 2019 Assessing the effects of sampling frequency on behavioural classification of accelerometer data. *J Exp Mar Biol Ecol* **512**, 22–30. (doi:10.1016/j.jembe.2018.12.003)

37. Korpimäki E, Wiehn J, Korpimaki E, Wiehn J. 1998 Clutch Size of Kestrels: Seasonal Decline and Experimental Evidence for Food Limitation under Fluctuating Food Conditions. *Oikos* **83**, 259. (doi:10.2307/3546837)

38. Lindström Å, Enemar A, Andersson G, Von Proschwitz T, Nyholm NEI. 2005 Density-dependent reproductive output in relation to a drastically varying food supply: getting the density measure right. *Oikos* **110**, 155–163. (doi:10.1111/J.0030-1299.2005.13828.X)

39. Robinson RA, Baillie SR, Crick HQP. 2007 Weather-dependent survival: implications of climate change for passerine population processes. *Ibis* **149**, 357–364. (doi:10.1111/J.1474-919X.2006.00648.X)

40. Plard F, Arlettaz R, Schaub M. 2018 Hoopoe males experience intra-seasonal while females experience inter-seasonal reproductive costs. *Oecologia* **186**, 665–675. (doi:10.1007/S00442-017-4028-8)

41. Almasi B, Roulin A, Jenni-Eiermann S, Jenni L. 2008 Parental investment and its sensitivity to corticosterone is linked to melanin-based coloration in barn owls. *Horm Behav* **54**, 217–223. (doi:10.1016/j.yhbeh.2008.02.021)

42. Dreiss AN, Henry I, Ruppli CA, Almasi B, Roulin A. 2010 Darker eumelanic barn owls better withstand food depletion through resistance to food deprivation and lower appetite. *Oecologia* **164**, 65–71. (doi:10.1007/s00442-010-1680-7)

43. Piault R, Gasparini J, Bize P, Jenni-Eiermann S, Roulin A. 2009 Pheomelanin-Based Coloration and the Ability to Cope with Variation in Food Supply and Parasitism. *Am Nat* **174**, 548–556. (doi:10.1086/605374)

44. Ducrest AL, Keller L, Roulin A. 2008 Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends Ecol Evol* **23**, 502–510. (doi:10.1016/J.TREE.2008.06.001)

45. San-Jose LM, Roulin A. 2018 Toward Understanding the Repeated Occurrence of Associations between Melanin-Based Coloration and Multiple Phenotypes. *Am Nat* **192**, 111–130. (doi:10.1086/698010)

46. Krüger O. 2002 Dissecting common buzzard lifespan and lifetime reproductive success: The relative importance of food, competition, weather, habitat and individual attributes. *Oecologia* **133**, 474–482. (doi:10.1007/S00442-002-1053-Y)

47. Bonier F, Martin PR, Moore IT, Wingfield JC. 2009 Do baseline glucocorticoids predict fitness? *Trends Ecol Evol* **24**, 634–642. (doi:10.1016/J.TREE.2009.04.013)

48. Béziers P, Korner-Nievergelt F, Jenni L, Roulin A, Almasi B. 2020 Glucocorticoid levels are linked to lifetime reproductive success and survival of adult barn owls. *J Evol Biol* **33**, 1689–1703. (doi:10.1111/JEB.13707)

49. Breuner CW, Patterson SH, Hahn TP. 2008 In search of relationships between the acute adrenocortical response and fitness. *Gen Comp Endocrinol* **157**, 288–295. (doi:10.1016/j.ygcen.2008.05.017)

50. Hau M, Ricklefs RE, Wikelski M, Lee KA, Brawn JD. 2010 Corticosterone, testosterone and life-history strategies of birds. *Proceedings of the Royal Society B: Biological Sciences* **277**, 3203–3212. (doi:10.1098/RSPB.2010.0673)

51. Martin K. 1995 Patterns and Mechanisms for Age-dependent Reproduction and Survival in Birds. *Integr Comp Biol* **35**, 340–348. (doi:10.1093/ICB/35.4.340)

52. Ball GF, Ketterson ED. 2007 Sex differences in the response to environmental cues regulating seasonal reproduction in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 231–246. (doi:10.1098/RSTB.2007.2137)

53. Cruz-Flores M, Pradel R, Bried J, González-Solís J, Ramos R. 2021 Sex-specific costs of reproduction on survival in a long-lived seabird. *Biol Lett* **17**, 20200804. (doi:10.1098/RSBL.2020.0804)

54. Gimenez O, Anker-Nilssen T, Grosbois V. 2012 Exploring causal pathways in demographic parameter variation: path analysis of mark-recapture data. *Methods Ecol Evol* **3**, 427–432. (doi:10.1111/j.2041-210X.2011.00150.x)

55. Béziers P, Roulin A. 2016 Double brooding and offspring desertion in the barn owl Tyto alba. *J Avian Biol* **47**, 235–244. (doi:10.1111/jav.00800)

56. Roulin A. 2020 *Barn Owls*. Cambridge University Press. (doi:10.1017/9781316694114)

57. Taylor IR. 1994 *Barn owls*. 1st edn. Cambridge: Cambridge University Press.

58. Roulin A. 2004 The function of food stores in bird nests: Observations and experiments in the Barn Owl Tyto alba. *Ardea* **92**, 69–78.

59. Tkadlec E, Zejda J. 1998 Small rodent population fluctuations: The effects of age structure and seasonality. *Evolutionary Ecology 1998 12:2* **12**, 191–210. (doi:10.1023/A:1006583713042)

60. Pavluvčík P, Poprach K, Machar I, Losík J, Gouveia A, Tkadlec E. 2015 Barn Owl Productivity Response to Variability of Vole Populations. *PLoS One* **10**, e0145851. (doi:10.1371/journal.pone.0145851)

61. Fay R, Michler S, Laesser J, Jeanmonod J, Schaub M. 2020 Large-Scale Vole Population Synchrony in Central Europe Revealed by Kestrel Breeding Performance. *Front Ecol Evol* **7**, 512. (doi:10.3389/FEVO.2019.00512)

62. Karell P, Ahola K, Karstinen T, Zolei A, Brommer JE. 2009 Population dynamics in a cyclic environment. *J Anim Ecol* **78**, 1050–1062. (doi:10.1111/j.1365-2656.2009.01563.x)

63. Tew TE, Macdonald DW. 1993 The effects of harvest on arable wood mice *Apodemus sylvaticus*. *Biol Conserv*. **65**.

64. Jacob J. 2003 Short-term effects of farming practices on populations of common voles. *Agric Ecosyst Environ* **95**, 321–325.

65. Heroldová M, Bryja J, Zejda J, Tkadlec E. 2007 Structure and diversity of small mammal communities in agriculture landscape. *Agric Ecosyst Environ* **120**, 206–210. (doi:10.1016/j.agee.2006.09.007)

66. Tattersall FH, Macdonald DW, Hart BJ, Manley WJ, Feber RE. 2001 Habitat use by wood mice (*Apodemus sylvaticus*) in a changeable arable landscape. *J Zool* **255**, 487–494. (doi:10.1017/S095283690100156X)

67. Todd IA, Tew TE, Macdonald DW. 2000 Arable habitat use by wood mice (*Apodemus sylvaticus*). 1. Macrohabitat. *J Zool* **250**, 299–303. (doi:10.1111/j.1469-7998.2000.tb00773.x)

68. El-Sabaawi R. 2018 Trophic structure in a rapidly urbanizing planet. *Funct Ecol* **32**, 1718–1728. (doi:10.1111/1365-2435.13114)

69. Varland DE, Bird DM, Negro Juan J. 1996 *Raptors in Human Landscapes*. Elsevier Science.

70. Shochat E, Lerman S, Fernández-Juricic E. 2015 Birds in Urban Ecosystems: Population Dynamics, Community Structure, Biodiversity, and Conservation. *Urban Ecosystem Ecology* , 75–86. (doi:10.2134/AGRONMONOGR55.C4)

71. Tscharntke T, Batáry P. 2023 Agriculture, urbanization, climate, and forest change drive bird declines. *Proc Natl Acad Sci USA* **120**, e2305216120. (doi:10.1073/pnas.230521612)

72. Bennett AF, Radford JQ, Haslem A. 2006 Properties of land mosaics: Implications for nature conservation in agricultural environments. *Biol Conserv* **133**, 250–264. (doi:10.1016/J.BIOCON.2006.06.008)

73. Séchaud R, Schalcher K, Machado AP, Almasi B, Massa C, Safi K, Roulin A. 2021 Behaviour-specific habitat selection patterns of breeding barn owls. *Mov Ecol* **9**, 1–11. (doi:10.1186/s40462-021-00258-6)

74. Arlettaz R, Krähenbühl M, Almasi B, Roulin A, Schaub M. 2010 Wildflower areas within revitalized agricultural matrices boost small mammal populations but not breeding Barn Owls. *J Ornithol* **151**, 553–564. (doi:10.1007/s10336-009-0485-0)

75. Aschwanden J, Birrer S, Jenni L. 2005 Are ecological compensation areas attractive hunting sites for common kestrels (*Falco tinnunculus)* and long-eared owls (*Asio otus*)? *J Ornithol* **146**, 279–286. (doi:10.1007/s10336-005-0090-9)

76. Williams CM, Henry HAL, Sinclair BJ. 2015 Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biological Reviews* **90**, 214–235. (doi:10.1111/BRV.12105)

77. Fretwell SD. 1972 *Populations in a seasonal environment*. Princeton, NJ: Princeton Univ. Pr.

78. Van Manen W. 2001 Influence of weather circumstances on behaviour and hunting success of wintering long-eared owls *Asio otus*. *Limosa* **74**, 81–86.

79. Kämpfer S, Engel E, Fartmann T. 2022 Weather conditions determine reproductive success of a ground-nesting bird of prey in natural dune grasslands. *J Ornithol* **163**, 855–865. (doi:10.1007/s10336-022-01999-w)

80. Jakosalem PGC, Collar NJ, Gill JA. 2013 Habitat selection and conservation status of the endemic Ninox hawk-owl on Cebu, Philippines. *Bird Conserv Int* **23**, 360–370. (doi:10.1017/S0959270912000317)

81. Cherry MJ, Barton BT. 2017 Effects of wind on predator-prey interactions. *Food Webs* **13**, 92–97. (doi:10.1016/J.FOOWEB.2017.02.005)

82. Lehikoinen A, Byholm P, Ranta E, Saurola P, Valkama J, Korpimäki E, Pietiäinen H, Henttonen H. 2009 Reproduction of the common buzzard at its northern range margin under climatic change. *Oikos* **118**, 829–836. (doi:10.1111/J.1600-0706.2008.17440.X)

83. Wróbel A, Bogdziewicz M. 2015 It is raining mice and voles: which weather conditions influence the activity of *Apodemus flavicollis* and *Myodes glareolus*? *Eur J Wildl Res* **61**, 475–478. (doi:10.1007/S10344-014-0892-2)

84. Wolton RJ. 1983 The Activity of Free-Ranging Wood Mice *Apodemus sylvaticus*. *J Anim Ecol* **52**, 781. (doi:10.2307/4453)

85. Hoogenboom I, Daan S, Dallinga JH, Schoenmakers M. 1984 Seasonal change in the daily timing of behaviour of the common vole, *Microtus arvalis*. *Oecologia* **61**, 18–31. (doi:10.1007/BF00379084)

86. Sipari S, Haapakoski M, Klemme I, Palme R, Sundell J, Ylönen H. 2016 Changing winter conditions in the boreal forest: the effects of fluctuating temperature and predation risk on activity and physiological stress level in bank voles. *Behav Ecol Sociobiol* **70**, 1571–1579. (doi:10.1007/S00265-016-2165-4)

87. Vautard R *et al.* 2014 The European climate under a 2 °C global warming. *Environmental Research Letters* **9**, 034006. (doi:10.1088/1748-9326/9/3/034006)

88. Lhotka O, Kyselý J, Farda A. 2018 Climate change scenarios of heat waves in Central Europe and their uncertainties. *Theor Appl Climatol* **131**, 1043–1054. (doi:10.1007/s00704-016-2031-3)

89. Dreiss AN, Antoniazza S, Burri R, Fumagalli L, Sonnay C, Frey C, Goudet J, Roulin A. 2012 Local adaptation and matching habitat choice in female barn owls with respect to melanic coloration. *J Evol Biol* **25**, 103–114. (doi:10.1111/j.1420-9101.2011.02407.x)

90. Charter M, Peleg O, Leshem Y, Roulin A. 2012 Similar patterns of local barn owl adaptation in the Middle East and Europe with respect to melanic coloration. *Biological Journal of the Linnean Society* **106**, 447–454. (doi:10.1111/j.1095-8312.2012.01863.x)

91. Le SEA, Durell VD. 2000 Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biological Reviews* **75**, 503–518. (doi:10.1111/J.1469-185X.2000.TB00053.X)

92. Roulin A. 2004 Covariation between plumage colour polymorphism and diet in the Barn Owl. *Ibis* **146**, 509–517. (doi:10.1111/j.1474-919x.2004.00292.x)

93. Mayr E. 1939 The Sex Ratio in Wild Birds. *Am Nat* **73**, 156–179. (doi:10.1086/280824)

94. Schalcher K. 2023 The use of high throughput wildlife tracking technology to study multiple aspects of barn owl movement ecology. PhD Thesis, University of Lausanne.

95. Stearns SC. 1989 Trade-Offs in Life-History Evolution. *Funct Ecol* **3**, 259. (doi:10.2307/2389364)

96. Barbraud C, Weimerskirch H. 2005 Environmental conditions and breeding experience affect costs of reproduction in Blue Petrels. *Ecology* **86**, 682–692. (doi:10.1890/04-0075)

97. Byholm P, Kekkonen M. 2008 Food regulates reproduction differently in different habitats: Experimental evidence in the goshawk. *Ecology* **89**, 1696–1702. (doi:10.1890/07-0675.1)

98. Erikstad KE, Fauchald P, Tveraa T, Steen H. 1998 On the cost of reproduction in long-lived birds: The influence of environmental variability. *Ecology* **79**, 1781–1788. (doi:10.2307/176796)

99. Sumasgutner P, Nemeth E, Tebb G, Krenn HW, Gamauf A. 2014 Hard times in the city: Attractive nest sites but insufficient food supply lead to low reproduction

rates in a bird of prey. *Journal of Wildlife Rehabilitation* **34**, 17–31. (doi:10.1186/1742-9994-11-48)

100. López-Calderón C, Hobson KA, Marzal A, Balbontín J, Reviriego M, Magallanes S, García-Longoria L, de Lope F, Møller AP. 2017 Environmental conditions during winter predict age- and sex-specific differences in reproductive success of a trans-Saharan migratory bird. *Sci Rep* **7**, 18082. (doi:10.1038/s41598-017-18497-2)

“ Of course I remember you, silly barn owl dude
*who can pop bottle tops off beers with absolutely *anything* ! “*

Prof. Dr. John Fieberg, October 2021