UNIL | Université de Lausanne

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

Year : 2021

Habitat selection and convergent evolution in the colour polymorphic barn owl

Séchaud Robin

Séchaud Robin, 2021, Habitat selection and convergent evolution in the colour polymorphic barn owl

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_46DF5BA439616

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

Département d'Ecologie et Evolution

Habitat selection and convergent evolution in the colour polymorphic barn owl

Thèse de doctorat ès sciences de la vie (PhD)

présentée à la

Faculté de biologie et de médecine
de l'Université de Lausanne

par

Robin SÉCHAUD

Master of Science in Behaviour, Ecology and Evolution
University of Lausanne

Jury

Prof. David Gatfield, Président
Prof. Alexandre Roulin, Directeur de thèse
Prof. Philippe Christe, Expert
Prof. Iain Couzin, Expert
Dr. Martin Grüebler, Expert

Lausanne
(2021)

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.	David	**Gatfield**
Directeur·trice de thèse	Monsieur	Prof.	Alexandre	**Roulin**
Expert·e·s	Monsieur	Prof.	Iain	**Couzin**
	Monsieur	Dr	Martin	**Grüebler**
	Monsieur	Prof.	Philippe	**Christe**

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

Monsieur Robin Séchaud

Maîtrise universitaire ès Sciences en comportement, évolution et conservation,
Université de Lausanne

intitulée

Habitat selection and convergent evolution in the colour polymorphic barn owl

Date de l'examen : 8 juillet 2021

Date d'émission de l'imprimatur : Lausanne, le 27 juillet 2021

pour le Doyen
de la Faculté de biologie et de médecine

Prof. Niko GELDNER
Directeur de l'Ecole Doctorale

Table of Contents

Remerciements

Cher Professeur A. Roulin, on dirait bien qu'on « est boc » pour de bon cette fois ! Alex, un immense merci de m'avoir fait confiance en me permettant de me lancer dans cet incroyable projet. Tu m'as laissé libre d'orienter mes recherches en fonction de mes intérêts, tout en faisant en sorte que les conditions soient réunies pour que ça se passe au mieux. J'ai particulièrement apprécié ton enthousiasme, ton dynamisme et ton franc-parler, et j'espère que tu continueras à faire profiter ton groupe de ces belles qualités.

J'aimerais également remercier chaleureusement les personnes qui font partie de mon comité de thèse et qui ont pris le temps de lire ce manuscrit et d'en discuter avec moi. Merci au Président du comité, David Gatfield, ainsi qu'aux trois experts Iain Couzin, Martin Grüebler et Philippe Christe.

Je crois que je ne pourrais jamais assez remercier toutes les personnes du groupe avec qui j'ai partagé tellement de choses. Spécialement Paul, qui m'a formé sur le terrain et qui a toujours été d'une aide précieuse ; Kim, qui a grandement contribué à développer ce super projet ; Luis, le grand sage qui m'a fait voir la science d'une autre manière. Merci à Andrea pour cette fructueuse collaboration, ainsi qu'à tous les autres membres du groupes, Pauline Who, Arnaud, Valérie, Anne-Lyse, Céline S., Vera, Paolo et Laurie pour leur soutien et les indispensables pause-café. Merci aux étudiants.es de master qui ont fortement contribué à la collecte de données, et plus particulièrement à Estelle, Planchette, Giulia et Steve avec qui j'ai pu continuer à travailler par la suite. Merci aussi à Charlène et Carolina qui étaient là pour le lancement du projet. J'ai aussi eu le privilège de collaborer avec Kami et Bettina, merci pour votre patience, votre soutien et vos encouragements. Il y a aussi Franck et Jason, qui ont assuré le soutien logistique indispensable à ces projets, merci !

Un immense merci également à Sacha et Sergio qui sont là depuis pas mal de temps, et avec qui on a fait tellement de trucs ~~débiles~~ inoubliables, vivement la suite ! Merci aussi à Sarah, qui s'est toujours dévouée pour terminer les gâteaux au chocolat à notre place. Un clin d'œil (brun ténébreux) à Laura, avec qui j'ai passé de supers moments à « jumeller » des piafs et à choper des « chauves ». Une petite pensée également pour toute l'équipe des « courent-batures » qui a dû m'écouter râler pendant 18h02min33s. Un sincère muchas gracias également à Alex, Philippe, Luca, Laurent W. et Francky pour ces expériences inoubliables.

J'aimerais aussi remercier Moineau, avec qui j'ai ouvert mes premiers nichoirs à Effraie, et qui m'a mis en contact avec Alex. J'ai aussi eu le privilège de pouvoir travailler avec des ornithologues et des agriculteurs·rices de toute la région qui ont contribué, d'une manière ou d'un autre, à l'avancement de mes projets de recherches, merci !

Un grand merci aussi à toute ma famille pour leur soutien et leur force. Vous mériteriez une pleine page pour vous, mais je vais plutôt réserver mes mots pour notre prochain apéro. J'ai de la chance de vous avoir. Merci !

Finalement, merci à Ana qui m'accompagnait sur le terrain pour qu'on puisse quand même passer un peu de temps ensemble. On a vécu des trucs mémorables, comme se retrouver aux urgences après s'être pris une échelle dans la tronche, ou aller mesurer des effraies congelées dans un musée en Crête pendant nos vacances … je me réjouis de vivre nos prochaines aventures !

Summary

Most species live in spatially and temporally heterogeneous environments, and local adaptation allows organisms to better exploit them by maintaining intra-specific genetic and phenotypic variation. Colour polymorphic species are ideal to study the selective pressures maintaining diversity, as well as the adaptive functions of the polymorphic trait. In the present thesis, I investigated the mechanisms maintaining colour polymorphism in the common barn owl *Tyto alba* at different scales and under different environmental conditions.

In the first two chapters, I studied resource selection using GPS tracking data of breeding barn owls in Switzerland. I showed that owls selected rare, but biodiversity-rich, areas in the habitat for hunting, and that males that had more of these in their home range had a higher breeding success. In addition, I provided a comprehensive breakdown of resource selection by barn owls during the reproductive season, and highlighted the importance of considering different scales in such analyses.

In the third and fourth chapters, I investigated whether barn owls with distinct plumage colourations were differently affected by moonlight. I showed that white barn owls performed better in moonlit nights than reddish individuals. In addition, I highlighted that, in moonlit nights, whitish owls foraged more in open habitats and induced longer freezing responses in prey which might facilitate their capture. This suggests that moon illumination might be involved in the evolution of colour polymorphism of nocturnal animals.

In the last two chapters, I examined the association between barn owl phenotypic traits and environmental conditions at the world scale. I showed that barn owl's plumage colouration was redder in colder and rainier regions, and was also related to the size of the prey consumed. I provided evidence that natural selection contributes to the convergent evolution of plumage colouration and body size in the different barn owl lineages.

In this thesis, I had the opportunity to address both applied and fundamental research questions by studying a widespread and colour polymorphic species. Finally, I highlighted how multi-scale analyses provide a wealth of opportunities to study the ecology and evolution of organisms from numerous perspectives.

Résumé

La plupart des espèces vivent dans des environnements spatialement et temporellement hétérogènes, et l'adaptation locale permet aux organismes de mieux les exploiter en maintenant la variation génétique et phénotypique intra-spécifique. Les espèces avec un polymorphisme de couleur sont idéales pour étudier les pressions sélectives qui maintiennent cette diversité, ainsi que les fonctions adaptatives du caractère polymorphique. Dans cette thèse, j'ai étudié les mécanismes de maintien du polymorphisme de couleur chez l'Effraie des clochers *Tyto alba* à différentes échelles et dans différentes conditions environnementales.

Dans les deux premiers chapitres, j'ai étudié la sélection des ressources en utilisant des données de suivi GPS d'Effraie des clochers se reproduisant en Suisse. J'ai montré que les chouettes chassaient dans des zones rares, mais riches en biodiversité, et que les mâles qui en avaient davantage dans leur domaine vital avaient un succès de reproduction plus élevé. J'ai également fourni une description complète de la sélection des ressources par l'Effraie des clochers pendant la saison de reproduction, et souligné l'importance de considérer différentes échelles spatiales dans de telles analyses.

Dans les deux prochains chapitres, j'ai cherché à savoir si les Effraies des clochers avec des couleurs de plumage différentes étaient affectées différemment par la lune. J'ai montré que les chouettes blanches étaient avantagées pendant les nuits avec une forte illumination lunaire. En outre, j'ai mis en évidence que, pendant les nuits fortement illuminées, les chouettes blanches chassaient davantage dans des habitats ouverts et que leurs proies restaient pétrifiées plus longtemps lors de l'attaque, ce qui pourrait faciliter leur capture. Cela suggère que l'illumination lunaire pourrait être impliquée dans l'évolution du polymorphisme de couleur chez des espèces nocturnes.

Dans les deux derniers chapitres, j'ai examiné l'association entre les traits phénotypiques de l'Effraie des clochers et les conditions environnementales à l'échelle mondiale. J'ai montré que la coloration du plumage de l'Effraie des clochers était plus foncée dans les régions froides et pluvieuses, et qu'elle était également liée à la taille des proies consommées. Cela souligne que la sélection naturelle contribue à l'évolution convergente de la coloration du plumage et de la taille du corps chez les différentes lignées de d'Effraies des clochers.

Dans cette thèse, j'ai eu l'occasion d'aborder des questions de recherche appliquée et fondamentale en étudiant une espèce répandue et qui présente un polymorphisme de coloration. J'ai pu mettre en évidence que des analyses à différentes échelles spatiales offrent une multitude de possibilités pour étudier l'écologie et l'évolution des organismes.

General Introduction

Local adaptation

Most species live in spatially and temporally heterogeneous environments, and local adaptation plays a crucial role in the maintenance of intra-species genetic and phenotypic variation (Gavrilets, 2003; Levene, 1953), as well as the variation in species geographical ranges (Guisan, Thuiller, & Zimmermann, 2017; Kirkpatrick & Barton, 1997). By definition, local adaptation predicts that resident individuals should have a better fitness in their local habitat than other individuals coming from elsewhere (Williams, 1966). It is generally due to the development, under natural selective pressure, of phenotypic traits conferring a selective advantage in the local environmental conditions. However, other evolutionary forces such as gene flow or genetic drift can hinder the selection for locally more adapted phenotypes (see the comprehensive review from Kawecki and Ebert 2004).

Local adaptation can be measured in different ways, the most rigorous of which consisting in comparing the fitness measured in the original habitat to that when transplanted elsewhere (Bradshaw, 1960; Hoeksema & Forde, 2008; Kawecki & Ebert, 2004). Alternatively, evidence of local adaptation can be provided by correlating a phenotypic trait expressed over multiple independent geographic regions to biologically relevant environmental features (Coop, Witonsky, Di Rienzo, & Pritchard, 2010; Hereford, 2009). Evidences for local adaptation have been discovered in different contexts, including camouflage (Hoekstra, Krenz, & Nachman, 2005; Mullen & Hoekstra, 2008), interspecific competition (Åbjörnsson, Hansson, & Brönmark, 2004; Grøndahl & Ehlers, 2008), host-pathogen interactions (Greischar & Koskella, 2007; Kaltz & Shykoff, 1998), soil toxicity (Gould, McCouch, & Geber, 2014; Jain & Bradshaw, 1966), altitude (Kim & Donohue, 2013; Muir, Biek, Thomas, & Mable, 2014) and temperature (Lonsdale & Levinton, 1985; McKay et al., 2001). Several general patterns have been shown to be consistent between taxa, such as the tendency for endotherm's body size to be larger in cooler regions, termed "Bergmann's rule" (Bergmann, 1847; Meiri, 2011). Thermoregulation is at the basis of this rule, with larger bodies having a lower surface-to-volume ratio limiting heat loss, resulting in a selective advantage for larger individuals in colder climates (e.g. higher elevations or latitudes). Finally, the specialization of some populations through strong local adaptation has the potential to lead to speciation (Kirkpatrick & Barton, 2006; Sobel, Chen, Watt, & Schemske, 2010).

Resource selection

Resource selection is a central concept in ecology, as it represents the requirements for an individual to survive and reproduce. As neither the resources, nor the organism's needs, are constant through space and time, individuals have to make choices over which resource to choose (Boyce, 2006). A common approach to measure resource selection consists in comparing the resources used by the animal to the ones available in the environment (Johnson, 1980; Manly, McDonald, Thomas, McDonald, & Erickson, 2002). By definition, if an animal doesn't make any choice about which resource to use (random resource selection), their use is expected to be proportional to their availability. Consequently, resources used disproportionally are considered to be selected or avoided if the selection exceeds or is inferior to the availability, respectively. As resource selection is a decision-making process, an underlying assumption is that natural selection will favour animals selecting best quality resources over bad ones (Michael L. Rosenzweig, 1981). However, resource quality alone is not sufficient to explain animal choices, as costs and benefits associated to their acquisition have to be considered (Hugie & Dill, 1994; M. L. Rosenzweig, 1985). For example, habitat selection has been shown to be influenced by predation (DeCesare et al., 2014; Jordan, Bartolini, Nelson, Patterson, & Soulen, 1997), competition (Cody, 1981; Hughes, Ward, & Perrin, 1994), food limitation (Dussault et al., 2005; McCollin, 1998) and anthropogenic disturbances (Ausprey & Rodewald, 2011; Bozek, Prange, & Gehrt, 2007). Consequently, as the presence of an animal in a given habitat might not be related to its quality, only the demonstration of an increased fitness associated to the selected habitats can guarantee its adaptive function (Mayor, Schneider, Schaefer, & Mahoney, 2009; Morris, 2003).

Resource selection is a scale-sensitive process that can fluctuate in time and space (Boyce, 2006; Mayor et al., 2009). The levels of selection can range from the geographic range of a herbivory species to which blade of grass to eat in a meadow, representing real challenges in term of analysis procedures and result interpretation (Bowyer & Kie, 2006; Johnson, 1980; McGarigal, Wan, Zeller, Timm, & Cushman, 2016). Defining the most pertinent temporal and spatial scale of analysis has always been a matter of debate, mainly because failure to detect selection at a given scale does not discount it at others (Bergin, 1992; Bowyer & Kie, 2006; Macdonald et al., 2018; Orians & Wittenberger, 1991). Consequently, conducting multi-scale resource selection studies has recently gained in popularity (Boyce, 2006; Mayor et al., 2009). In a first attempt to propose a unified multi-scale resource selection framework, Johnson (1980) proposed four specific orders of selection : species range, home range, foraging site and food item. Practically, scales are mainly defined according to the species of interest, the environment type and the granularity of the data collected (Mayor et al., 2009).

Movement

Organisms' movement, aiming at satisfying their requirements in term of reproduction and survival, is a central concept of almost all ecological and evolutionary processes (Jeltsch et al., 2013; Nathan et al., 2008). Movement affects species distributions and interactions (Pagel & Schurr, 2012; Schweiger et al., 2012), population dynamics and genetics (Cushman & Lewis, 2010; Hanski, Kuussaari, & Nieminen, 1994; Shafer et al., 2012), habitat characteristics and resource levels (Jefferies, Jano, & Abraham, 2006; Stapp, Polis, & Sánchez Piñero, 1999). Studying the motivation, physical mechanism and functional adaptation associated to animal movement, as well as the external factors influencing it, is of prime interest because they represent the processes at the basis of movement (Holyoak, Casagrandi, Nathan, Revilla, & Spiegel, 2008; Jeltsch et al., 2013; Nathan et al., 2008; Sutherland et al., 2013). Practically, understanding these movement mechanisms allows to anticipate the spread of diseases (Daversa, Fenton, Dell, Garner, & Manica, 2017; Van Moorter et al., 2013) or, in the context of human-caused environmental changes, to propose targeted conservation measures (A. M. Allen & Singh, 2016; Fraser et al., 2018).

Animals movement has fascinated mankind for a long time, and John James Audubon in 1803 was the first to conduct an animal tracking experiment by attaching silver wires to the legs of birds in order to study migratory behaviour (Davis, Jackson, & Tautin, 2008). Since then, tracking technologies have developed and it became common to attach electronic tags, such as GPS devices, to animals to track their movements (Cochran & Lord, 1963; Gibbons & Andrews, 2004; Nathan et al., 2008). The latest generation of tracking devices can record the movement of an animal throughout most of its life with an increased spatiotemporal resolution, while being coupled with secondary sensors collecting additional body positioning, physiological or environmental information (Kays, Crofoot, Jetz, & Wikelski, 2015). This huge amount of raw movement data collected offers unmatched research opportunities, while being accompanied by unprecedented challenges in data storage, management and analysis. In this context, Nathan et al. (2008) pointed out that, when analysing the data, "the greatest challenge is to identify the proximate and ultimate drivers that break up the path into different movement phases". In the last decades, analytical tools segmenting a movement trajectory into behavioural modes have flourished, with different levels of complexity and *a priori* assumptions on behavioural mode characteristics (Benhamou, 2004; Fauchald & Tveraa, 2003; Garriga, Palmer, Oltra, & Bartumeus, 2016; Roberts, Guilford, Rezek, & Biro, 2004; Thiebault & Tremblay, 2013). By segmenting a trajectory into behavioural modes, it becomes possible to identify the underlying fine-scale ecological mechanisms driving the choices made by an animal along its path (Kays et al., 2015; Nathan et al., 2008). Under the current rapid human-caused environmental changes, identifying such mechanisms and requirements acting at the behavioural level might be crucial for the development of efficient conservation measures (Roever, Beyer, Chase, & van Aarde, 2014; Suraci et al., 2019).

Colour polymorphism

Polymorphism is the coexistence in the same population of two or more genetically determined forms of the same species, the rarest morph being too frequent to be only the result of recurrent mutation (Ford, 1945; Huxley, 1955). The morphisms only related to sex, age, body condition or seasonality are not considered as polymorphism (Huxley, 1955). Various behavioural (Lank, Smith, Hanotte, Burke, & Cooke, 1995; Zimmerer & Kallman, 1989), physiological (Simpson, Jackson, & Herrera-Cubilla, 2017; Smith, 1987) and morphological (Chappell & Snyder, 1984; Dong et al., 2017) polymorphisms have been reported, from a wide range of taxa. By definition, morphs have different selective advantages and disadvantages maintaining a certain balance (Huxley, 1955), which can fluctuate according to environmental variations (Kettlewell, 1955, 1956). Thus, polymorphic species are of prime interest for evolutionary biologists in the study the evolution and maintenance of genetic and phenotypic diversity (Darwin, 1859; Ford, 1945; Huxley, 1955; McKinnon & Pierotti, 2010; Roulin, 2004b).

Colour polymorphism is found in many animals (E. A. Hoffman & Blouin, 2000; Roulin & Wink, 2004) and plants (Armbruster, 2002; Brown & Clegg, 1984). As colouration plays multiple functions, from camouflage to sexual ornamentation, morphs have been shown to differ in thermoregulation (Clusella Trullas, van Wyk, & Spotila, 2007; Hetem et al., 2009), background matching (Majerus, Brunton, & Stalker, 2000; Tsurui, Honma, & Nishida, 2010), habitat selection (Ahnesjö & Forsman, 2006; Muri et al., 2015), foraging success (Greco & Kevan, 1999; Tso, Tai, Ku, Kuo, & Yang, 2002), hunting technique (Sievert Rohwer, 1990) or anti-predator strategy (Losey, Ives, Harmon, Ballantyne, & Brown, 1997). Spatially, different colour morphs can coexist in the same place at the same time, but can also be distributed along a cline (Antoniazza, Burri, Fumagalli, Goudet, & Roulin, 2010; J. I. Hoffman et al., 2018).

The use of the term "morphs" can be misleading because, although some polymorphisms are composed of a number of distinct morphs (McKinnon & Pierotti, 2010; Pryke, Astheimer, Buttemer, & Griffith, 2007), others are rather characterized by a continuous morphism (Huxley, 1955; Roulin, 2004b). In the second case, colour variation can either be quantified on a continuous scale, or simplified by arbitrarily dividing the continuum into morphs. However, considering a polymorphism as a gradient between two extremes or as distinct morphs influences greatly the understanding of its adaptive function, and thus the genetic basis of its evolution and maintenance (Roulin, 2004b).

Research on colour polymorphism increased rapidly in the last two decades (Forsman, 2016), with three main perspectives. First, evolutionary biologists used colour polymorphism to explore the evolutionary processes underlying the development of genetic and phenotypic diversity (McKinnon & Pierotti, 2010; Svensson, 2017). Second, the coexistence of different morphs in the same population allowed to study the selective pressures maintaining such diversity (Passarotto, Parejo, Penteriani, & Avilés, 2018; Roulin, 2004b). And third, coexisting morphs provide a powerful set-up to study the adaptive function of the polymorphic trait (Galeotti, Rubolini, Dunn, & Fasola, 2003; Klinka & Reimchen, 2009).

Several hypotheses have been formulated to explain the evolution and maintenance of colour polymorphism (reviewed in Galeotti et al. 2003; Roulin 2004), but two of them received the most support: apostatic and disruptive selection. First, apostatic selection, or negative frequency-dependant selection, is based on prey-predator interactions (J. A. Allen, 1988; Paulson, 1973; S. Rohwer & Paulson, 1987). In the case of a colour polymorphic predator, it postulates that the prey is the selective agent as its visual cues will be less able to recognize a rare morph, and thus be more prone to be predated by it. Similarly, a new morph in a prey species population can spread because it will be less targeted or detected by predators, which are used to search for the common morph. From an evolutionary perspective, this mechanism could also explain the initial spread of a new colour variant in a population. While the foraging advantage benefited by the rare morph may allow it to spread through the population, an equilibrium will be reached when morphs will be equally detected by their prey (Bond & Kamil, 1998). The second hypothesis, termed as disruptive selection, postulate that selective pressure might, under different environmental conditions, favour extreme morphs over intermediate ones (Mather, 1955; Rueffler, Van Dooren, Leimar, & Abrams, 2006). Environmental heterogeneity is thus a prerequisite for disruptive selection to occur, with different morphs exploiting different ecological niches (Skulason & Smith, 1995). The drivers of disruptive selection are many and varied, and colour morphs have been shown to differ in reproductive strategies (Roulin, Ducret, Ravussin, & Altwegg, 2003), climatic preferences (Hill & McGraw, 2006), habitat selection (Muri et al., 2015), foraging technique (Sievert Rohwer, 1990) and prey consumption (Roulin & Wink, 2004).

In birds, colour polymorphism is relatively rare as it has been found in 3.5% of the species only (Galeotti et al., 2003). However, colour polymorphic species are present in 61% of the bird orders and 37% of the families, irrespectively of phylogeny. This suggests that colour polymorphism evolved independently in different bird taxa, and thus provides a favourable setting to study convergent evolution. Most polymorphic species have been shown to live in heterogeneous habitats and to be predators (carnivorous, insectivorous or piscivorous) and, among the different orders, Strigiformes (owls and nightjars) contained the highest percentage of polymorphic species (33.5%). Finally, Galeotti et al. (2003) argued that the disruptive selection hypothesis may be the primary force maintaining colour polymorphism in birds, and that habitat structure and varying light conditions are the most important selective mechanisms.

The common barn owl

Common barn owls colonized all continents except Antarctica and exploit a broad range of habitats, from desert-like landscapes to tropical forests. The composition of its diet varies in relation to the environment. While small mammals compose invariably the vast majority of the diet, other species can be consumed in varying proportions, such as birds, reptiles, amphibians or invertebrates (Roulin, 2020; Taylor, 1994). Although the morphology of the common barn owl is globally similar among its distribution range, local adaptations shaped differences in body size and plumage colouration (Taylor, 1994). The "common barn owl" denomination refers to a complex with a varying number species and subspecies that differ in body size, plumage coloration and geographical distribution (Uva, Päckert, Cibois, Fumagalli, & Roulin, 2018). In light of the most recent phylogenetic reconstructions (Aliabadian, Alaei-Kakhki, Mirshamsi, Nijman, & Roulin, 2016; Uva et al., 2018; Wink, El-Sayed, Sauer-Gürth, & Gonzalez, 2009), most subspecies were not supported and only three distinct evolutionary lineages were identified : the Afro-European barn owl (*Tyto alba*), the Australasian barn owl (*T. javanica*) and the American barn owl (*T. furcata*). These lineages display a wide range of local adaptations, providing a unique opportunity to study convergent evolution at the world scale.

As a colour polymorphic species, the common barn owl displays two distinct melanin-based plumage colour polymorphisms (Roulin, 2003). First, its ventral plumage colouration ranges from white to dark reddish-brown, with all possible intermediate tones. Second, it can be immaculate or ornamented with black dots of varying sizes. These plumage colour traits are genetically-determined and have been associated with different life-history traits and predator-prey interactions (Antoniazza et al., 2010; A. N. Dreiss et al., 2016; Roulin, 2004a; Roulin & Altwegg, 2007). In Europe, barn owls (*Tyto alba*) display a striking plumage colour cline, which varies from white in Iberia to dark rufous in North-eastern Europe (Antoniazza et al., 2010; Roulin & Dijkstra, 2003). In two key papers, Antoniazza et al. (2010, 2014) showed that barn owls recolonized Europe from Iberia after the last glacial period, and that the colour polymorphism as observed today is maintained by selection. Although the extreme morphs are predominant at the edge of the cline, the different colour morphs coexist in the same environment along the cline and thus provide ideal conditions to study local adaptation and selection mechanisms maintaining colour polymorphism. A first evidence of disruptive selection acting at a local scale was provided by Roulin (2004a) and Charter et al. (2012) who showed that reddish individuals feed primarily on common voles (*Microtus arvalis*) and whiter ones on wood mice (*Apodemus* spp.). Whether this selective prey capture is a choice made by the owl or an indirect effect related to a morph specific habitat use or detection by prey still has to be investigated. Recently, Dreiss et al. (2012) provided evidence for colour-dependant nest site selection, with reddish females breeding in sites surrounded by more arable fields and less forests than whitish ones, associated with fitness benefits in term of number of fledglings produced. While the adaptive function of each morph remains uncertain, these previous studies suggest a role in the detectability of the owl by its prey in relation to habitat features.

Aim and outline of the thesis

The aim of this thesis is to better understand the mechanisms maintaining colour polymorphism in the barn owl at different scales, from morph-specific behavioural response to varying local conditions, to the convergent evolution of plumage colouration at the worldwide scale. To achieve this goal, I combined fine scale GPS tracking data of almost 500 breeding barn owls in Switzerland, and data from more than 10’000 barn owl skins collected in museums from the entire distribution range of the common barn owl group.

In the first chapter, we studied barn owl resource selection in Swiss farmland at various scales by tagging them with GPS devices during the breeding season. Specifically, we explored the association between behavioural mode and habitat structure, with the expectation that resource selection will differ in relation to the needs associated to the behavioural modes. To appropriately evaluate the use of rare and scattered habitats, we used cutting edge resource selection analyses which redefine the habitats available to an animal according to its current location. Taking advantage of this, we investigated the use by barn owls of several types of agri-environment schemes (AES) implemented in the study area to maintain and promote biodiversity in farmland.

In the second chapter, we explored how habitat use and home range size, which is a proxy of habitat quality, affect male hunting behaviour and parental investment during the rearing period, and how such a parental effort translates into offspring pre-fledging survival and quality. We also tested two competing hypotheses about male investment when living in low-quality habitats. First, increasing their effort in order to improve nestlings’ survival and therefore their current reproductive success, while paying an energetic cost with potential negative consequences on future reproduction. Second, limiting their effort in order not to compromise survival and future reproduction, but possibly compromising their current reproductive success.

In the third chapter, we investigated whether barn owls with distinct plumage colourations are differently affected by moonlight. Combining data from long-term population monitoring with high resolution GPS tracking, we explored the influence of the moon illumination on barn owl colour morphs hunting success, food provisioning and breeding success. To identify the mechanism behind colour-specific performance in barn owls, we experimentally investigated the antipredator response of the barn owls' main prey, the common vole, when exposed to white and red owls under different moonlight conditions.

In the fourth chapter, we studied the effect of moon illumination on fine-scale barn owl habitat use and prey capture. Moonlight creates illuminated or shaded areas in the habitat, and barn owls with distinct plumage colourations might select one or the other of these conditions to maximize their hunting success. Using GPS tracking data, we investigated changes in near-forested habitat selection, the main habitat type producing light heterogeneity in the study area, depending on the moon illumination. As prey may also adapt their activity and behaviour depending on the moonlight, or detect one of the morphs more easily than the other, we recorded the prey caught by the different morphs in varying light conditions.

In the fifth chapter, we used barn owl skins collected in museums to describe the observed worldwide geographical variation in plumage colouration, and to examine whether the degree of melanism varies with latitude and between hemispheres. Then, we investigated the association between barn owl plumage colour and climatic factors, and related the results with general biogeographical rules. Under a scenario of convergent evolution, we expected similar relationships between colour traits and climatic factors among Afro-European, American and Australasian barn owls.

In the sixth and final chapter, we examined the association between barn owl phenotypic traits and diet composition at the world scale. In particular, we investigated whether body size and plumage colouration vary geographically according to diet features, such as percentage of mammals, prey size and diversity. As it has been shown for other species, we propose that the interactions between the barn owls and their prey are important drivers of the evolution of local adaptation shaping the spatial phenotypic variation currently observed in this species.

Chapter 1

Behaviour-specific habitat selection patterns of breeding barn owls

Robin Séchaud[1], Kim Schalcher[1], Ana Paula Machado[1], Bettina Almasi[2], Carolina Massa[1,3,4], Kamran Safi[5,6†] and Alexandre Roulin[1†]

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

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

[3] Instituto de Investigación e Ingeniería Ambiental, Laboratorio de Ecología de Enfermedades Transmitidas por Vectores, Universidad Nacional de San Martín, 25 de Mayo, 1650 San Martín, Buenos Aires, Argentina.

[4] Inmunova S.A., 25 de Mayo, 1650 San Martín, Buenos Aires, Argentina.

[5] Max Planck Institute of Animal Behaviour, Department of Migration, Am Obstberg 1, Radolfzell, 78315, Germany.

[6] University of Konstanz, Department of Biology, Universitätsstraße 10, Konstanz, 78464, Germany.

[†] Co-senior authors.

Chapter Status:

Published in Movement Ecology

https://doi.org/10.1186/s40462-021-00258-6

Author contributions:

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

Séchaud *et al. Movement Ecology* (2021) 9:18
https://doi.org/10.1186/s40462-021-00258-6

Movement Ecology

RESEARCH Open Access

Behaviour-specific habitat selection patterns of breeding barn owls

Robin Séchaud[1*], Kim Schalcher[1], Ana Paula Machado[1], Bettina Almasi[2], Carolina Massa[1,3,4], Kamran Safi[5,6†] and Alexandre Roulin[1†]

Abstract

Background: The intensification of agricultural practices over the twentieth century led to a cascade of detrimental effects on ecosystems. In Europe, agri-environment schemes (AES) have since been adopted to counter the decrease in farmland biodiversity, with the promotion of extensive habitats such as wildflower strips and extensive meadows. Despite having beneficial effects documented for multiple taxa, their profitability for top farmland predators, like raptors, is still debated. Such species with high movement capabilities have large home ranges with fluctuation in habitat use depending on specific needs.

Methods: Using GPS devices, we recorded positions for 134 barn owls (*Tyto alba*) breeding in Swiss farmland and distinguished three main behavioural modes with the Expectation-Maximization binary Clustering (EMbC) method: perching, hunting and commuting. We described barn owl habitat use at different levels during the breeding season by combining step and path selection functions. In particular, we examined the association between behavioural modes and habitat type, with special consideration for AES habitat structures.

Results: Despite a preference for the most common habitats at the home range level, behaviour-specific analyses revealed more specific habitat use depending on the behavioural mode. During the day, owls roosted almost exclusively in buildings, while pastures, meadows and forest edges were preferred as nocturnal perching sites. For hunting, barn owls preferentially used AES habitat structures though without neglecting more intensively exploited areas. For commuting, open habitats were preferred over wooded areas.

Conclusions: The behaviour-specific approach used here provides a comprehensive breakdown of barn owl habitat selection during the reproductive season and highlights its importance to understand complex animal habitat preferences. Our results highlight the importance of AES in restoring and maintaining functional trophic chains in farmland.

Keywords: Agri-environment schemes, AES, Global positioning system technology, GPS, Home range, Path selection, Step selection, *Tyto alba*

---

* Correspondence: robin.sechaud@unil.ch
[†]Kamran Safi and Alexandre Roulin are co-senior authors.
[1]Department of Ecology and Evolution, University of Lausanne, Building Biophore, CH-1015 Lausanne, Switzerland
Full list of author information is available at the end of the article

Introduction

The intensification of agricultural practices over the past century has severely changed European farmland [1, 2]. Many animal and plant populations declined [3, 4], and agriculture itself is suffering from the loss of services provided by wild organisms, such as crop pollination [5]. To counter the strong decrease in farmland biodiversity, European countries have adopted agri-environment schemes (AES), consisting mainly of paying direct subsidies to farmers to implement environmentally friendly farming practices. Despite documented beneficial effects on plant, insect and small mammal densities and on species richness [6–8], the effects of AES for larger vertebrate species remain unexplored. Probably the wide range of habitat used and movement capabilities render these species difficult to study. However, ensuring the presence of large vertebrate species, such as raptors, is an important step in the process of restoring and maintaining functional food chains in farmland ecosystems [9].

Distinguishing fine scale habitat preferences associated with different behaviours is key for understanding the underlying biological processes that drive animal movement [10]. How an animal uses its habitat is a complex decision-making process that can fluctuate with various factors, such as food availability [11], season [12], and individual life history traits [13], but also with the spatial and temporal scale considered [14, 15]. Habitat selection based on different behavioural modes has so far received limited attention, but the recent development in animal tracking technologies generated the opportunity to collect GPS locations at a high enough frequency to infer an animal's behaviour from it [16–18]. Including a behavioural component in habitat selection analyses may be particularly valuable for depicting behaviour-specific selection patterns and consequently for improving prioritization in habitat management and conservation [10, 19].

The barn owl (*Tyto alba*), a raptor hunting small mammals in farmlands, suffered a rapid decline across Europe, mainly due to the spread of urbanization and the intensification of farming practices affecting the availability of nesting sites and quality of foraging habitats [20, 21]. While providing nest boxes relieved the shortage of secure breeding sites, the knowledge on habitat requirements is still patchy. A previous study did not find any association between nest box occupancy, reproductive success and the surrounding habitats [22], indicating that habitat preferences may occur at a finer scale within the home range. In a radio tracking study, Arlettaz et al. (2010) showed that foraging activity was more intense in cereal crops and grasslands than in more extensively exploited areas, suggesting that AES could be less important for farmland raptors than suspected.

Here, to explore the association between behavioural modes and habitat structure, we studied behaviour-specific habitat selection in wild barn owls breeding in an intensive agricultural landscape in western Switzerland. We expect barn owls to select different habitat structures according to the needs associated to the different behavioural modes. Over 2 years, we equipped barn owl breeding pairs with GPS devices. Combining the high location sampling rate with a behavioural segmentation method, we distinguished three main behavioural modes - perching, hunting and commuting – and related them with habitat use. These behavioural modes represent three main movement behaviours displayed by barn owls outside of their nests (their definition and manner distinction are further explained in the methods). To appropriately evaluate the use of rare and scattered habitats, as is the case with AES, we used step and path selection functions, which define the habitats available to an animal according to its current location. In this context, AES habitats might not be recognisably selected at the home range level but they can still be important components of barn owl behaviour-specific habitat use and possible key elements for farmland raptors.

Materials and methods

Study area and barn owl population monitoring

The study was carried out in 2016 and 2017 in a 1,000 km^2 intensive agricultural landscape in western Switzerland where a wild population of barn owls breeds in nest boxes attached to barns [22]. In the first 2 weeks after hatching, the adult females remain almost entirely in the nest to provide warmth to their offspring and distribute the food among them brought by the male. After this period, both parents hunt small mammals, the male being the main contributor to the feeding of the nestlings [23].

GPS tags and deployment

We used GiPSy-5 GPS tags (Technosmart, Italy) weighing approximately 12 g including battery (less than 5% of the owl body mass; in our population, body mass ranged from 251 to 393 g), measuring 30x20x10 mm including the battery, and coupled with a 40 mm long antenna. They were attached as backpacks with a Teflon harness. Each tag collected location and time every 10 s, from 30 min before dusk until 30 min after dawn, covering the entire owl nocturnal activity period.

Breeding barn owls were captured at their nest site when the oldest offspring was 25 days-old on average (SD = 2.8), equipped with GPS tags and released at the capture site. We recorded adults' sex and age (categorized as yearlings or older birds). Approximately 2 weeks later, the owls were recaptured and the GPS tags recovered. The deployment of GPS tags corresponds to a period of intense habitat use by the parents to feed their nestlings, while being in accordance with ethical (earlier captures could lead to the abandonment of the clutch) and methodological constraints (later recapture could be compromised due to changes in food provisioning behaviour). Prior to any analysis, the 134 GPS tracks (72 males and 62 females) were filtered for aberrant positions using speed (excluding locations with a speed higher than 15 m/s) and location (excluding locations outside the study area). From the 1,924,623 collected positions, 1,922,636 were kept for the following analyses (1987 removed).

Habitat monitoring

Once a barn owl breeding pair was equipped with GPS tags, we mapped the habitat at high-resolution in a radius of 1.5 km around the nest site and stored the surveys in QGIS v.2.18.13 [24]. The 7 km^2 mapped corresponded to barn owl home range sizes reported in the literature (range: 0.9–8.1 km^2) [21, 23, 25]. When barn owls travelled out of the area initially mapped, we went to the field to map it shortly after the GPS tag recovery. We adopted a 10-category habitat classification (Table S1), with 6 categories recorded directly in the field - cereals, root vegetables (sugar beets and potatoes), pastures, intensive meadows, extensive meadows and wildflower strips – and the four remaining categories – forests, forest edges, roads and settlements – were derived from the swissTLM^{3D} catalogue (Swiss Topographic Landscape Model). The cereals, root vegetables, intensive meadows and pastures habitat categories represent the intensive agricultural land use, whereas the wildflower strips and extensive meadows are AES implemented in the area to preserve and promote biodiversity in farmland (Table S2). Forests are common structural components of this landscape, and their edges are transitional zones between the forested areas and the crops. Finally, the farmland landscape is interspersed with anthropogenic constructions, which are represented here by the road and settlement habitat categories.

Behaviour annotation

Barn owl movement data were classified into different behavioural modes using the Expectation-Maximization binary Clustering (EMbC) method implemented in the *EMbC* package [18]. EMbC is an unsupervised algorithm that clusters movement data based on speed and turning angle between locations. The three behavioural modes distinguished were perching, hunting and commuting. Perching, as a stationary behaviour, was characterized by low speed and a wide range of turning angles due to little GPS location errors. Hunting was characterized by low-medium speed and medium-high turning angles, whereas commuting was characterised by fast and straight flights. For validation, the EMbC behavioural classification was confronted to a visual classification performed on the tracks of 20 individuals. We found an average match of 92.7% between the visual and the EMbC classifications (perching: mean = 94.5%, SE = 2.3; hunting: mean = 92.6%, SE = 4.9; commuting: mean = 91.1%, SE = 3.8; San-Jose et al. 2019). These and all subsequent analyses were conducted with R v3.5.1 [26].

Home range size and composition

Home range size was calculated using a 95% kernel density estimator method [27]. To deal with temporal auto-correlation between data points, we used the continuous-time movement modelling package (*ctmm*) [28] to calculate home range size via auto-correlated kernel density estimation (AKDE) [29]. The ctmm model was calibrated using User Equivalent Range Error (UERE), estimated with location data obtained by fixed GPS devices in open landscape. Model parameters with better fit were chosen automatically with the function *variogram.fit* in the *ctmm* package [28]. Barn owl home range composition was obtained by extracting the relative abundance of the 10 habitat categories contained in each home range.

We modelled the effect of sex and age, as well as year and date of GPS data collection, on the home range size of the barn owls using a linear mixed-effect model parametrized with the lmerTest package [30]. The home range size was log-transformed and the brood ID, grouping owls belonging to the same brood, set as random factor. For all linear mixed-effect models used in this paper, we checked for collinearity between predictors and verified the assumptions of Gaussian error distribution by visually inspecting residual diagnostic plots.

Habitat selection

Home range selection

Home range selection (positioning of the home range in the landscape) compared the composition of the habitats available in the landscape, defined as the habitats contained in the 1.5 km radius around the nest site, with the ones contained in the home ranges (third-order selection; [31]), using *ADEhabitatHS* package [32]. For this and all subsequent analyses, selection ratios were estimated for each individual and habitat category, and then averaged to obtain the population's habitat selection estimates. In addition, when some habitat selection coefficients were poorly estimated (because the habitats were absent or rare), we re-ran the model without the problematic habitat category to avoid misestimating the other selection estimates (Table S3).

Roosting and perching site selection

Roosting and perching site selection were analysed separately, with the former representing the sites used for hiding and resting during the day and the latter the sites used to perch during the night-time activity. Roosting site selection analyses compared the roosting sites' habitats used to the ones available in the home range (third-order selection; [31]).

Perching site selection analyses compared night perching sites' habitats to the ones available in the home range (third-order selection; [59]). Rather than considering each perching location point independently, they were grouped into perching events. As the choice of a perching site may depend on the surrounding landscape (perching sites corresponding to the nest site were excluded from the analyses), the habitat types present within a 100 m radius around the perching site were extracted.

Hunting ground selection

We parametrized a step selection function (SSF) to identify how habitat influences barn owl hunting movements [33]. The SSF considers the choice made by the animal at each step by comparing the observed step to a set of alternative ones, thus redefining the available habitats at every step. Using the *ctmm.fit* function in the *ctmm* package [28], we calculated that 30-s step time intervals were characterised by weak autocorrelation between steps, while maintaining sufficient resolution to address how habitat is selected during hunting. Once thinned to 30-s intervals, each observed step was paired with 100 alternative steps generated by randomly picking the step lengths (distance between successive locations) and turning angles (change in direction between steps) from the distribution of these parameters for the entire population using the *amt* package [34]. The habitat at the end point of each of these alternative steps was extracted. To compare habitat characteristics of observed and random steps, we ran a conditional logistic regression with *amt*'s *fit_clogit* function. The models contained 8 habitat categories – cereals, root vegetables, forests, forest edges, intensive meadows, extensive meadows, pastures and wildflower strips – as well as three movement parameters – step length, log of the step length and the cosine of the turning angle –known to render the estimates of the habitat regression parameters more robust [35, 36]. Including these movement variables as predictors allow to model both movement and habitat selection processes into an *integrated step selection function* [36]. The step and burst IDs were entered as strata in the model, the first one to link the real and the 100 alternative steps and the second one to group the steps belonging to the same track. Two habitat categories – roads and settlements – were not included in the models because they were too rare in the dataset and prevented the models from converging.

To investigate if the similarity in habitat selection coefficients between individuals was related to seasonality and individual factors, we used a non-metric multidimensional scaling approach (NMDS; [37]). NMDS is a rank-based ordination method that uses pairwise distances between objects or individuals, and represents them in a low dimensional space. Using the coefficients of selection, a dissimilarity matrix was built with the Bray-Curtis method using the function *metaMDS* in the *vegan* package [38]. The wildflower strips habitat category was removed from this analysis because the limited number of coefficients obtained was not sufficient to parameterize a valid NMDS model (Table S3). To investigate if the year and date of GPS data collection, as well as the sex and the age of the owl, could explain the similarity or differences between birds in the classification proposed by the NMDS, we ran a permutation test using the *envfit* function in the same package with 10,000 permutations. We included in the model the year and date of GPS data collection as proxies for temporal variations in the landscape structure and profitability.

Commuting path analyses

Commuting tracks were classified in three main categories, each with a different purpose. The first type of commuting flight takes place when an owl leaves its nest box to reach a hunting ground or a perching spot. The second one is the reverse, when the owl catches a prey item and returns to the nest box to feed its nestlings. The third type of commuting is used to move within the landscape, to travel between hunting or perching sites, and is independent from the nest box location.

We built a path selection function (PathSF) to investigate the influence of landscape on commuting flights [39]. In PathSF, the entire path is the unit of measurement and, in a similar fashion to SSF, is compared to randomly generated paths. We discarded the commuting to and from the nest box to avoid the bias associated to the habitats surrounding the nest box location, and therefore considered only the commuting flights within the habitat. For each observed path, 20 alternative paths were generated by first randomly relocating the starting point of the path within a radius of 1.5 km, and then by rotating it by a random angle between 0 and 360 degrees [39]. Habitats contained in a 20-m buffer along the tracks were extracted and, to compare observed and random paths, conditional logistic regressions were built using the *fit_clogit* function in the *amt* package [34]. For statistical purposes, we grouped cereals, vegetable roots, pastures and intensive meadows into an "intensive open habitats" category, while the categories extensive meadows and wildflower strips were aggregated into "extensive open habitats". We built conditional logistic regression models containing intensive open habitats, extensive open habitats, forests, forest edges and roads as explanatory variables, and the burst ID as strata. Settlements were excluded from the analyses because they were under-represented in the extracted habitats and caused models to not converge.

For each of the three commuting flight types, the deviation from the straightest path was measured as the difference between the length of the real track and that of the shortest path between the starting and ending point of the commuting event. To test if the distance covered, the deviation from the straightest path, and the speed (calculated as the distance covered divided by the time) differed between the three types of commuting, we ran linear mixed-effect models using the *lmerTest* package [30]. The distance covered and the deviation from the straightest path were log-transformed. The type of commuting was entered as an explanatory variable and the bird identity set as random factor.

Results

Behaviour characteristics and activity period

For the 134 individuals considered (72 males and 62 females), the number of nights with data recorded varied between 4 and 15 (mean = 9.9; SD = 2.1) and the time interval between each location was 9.9 s on average (SD = 1.3). Behavioural annotation of the GPS tracks (sampling every 10 s) revealed great differences in step lengths and turning angles between perching, hunting and commuting behavioural modes (Fig. S1). Hunting flights were performed at an average speed of 4.9 m/s (SD = 1.0; range: 1.7–12.2 m/s), while the mean speed of commuting flights was 6.6 m/s (SD = 1.1; range: 2.4–13.4 m/s). Occasionally, owls flying at speeds above 10 m/s were recorded when commuting (max = 13.4 m/s), for a flight duration from 50 s to 9 min (Fig. S2).

The nightly activity period, defined as the time between two daylight roosting events, varied from 5.4 min to 10.4 h (median = 6.8 h, SD = 2.1; Fig. S3). During their activity period, barn owls perched on average 77.5% (SD = 13.8; range: 14.6–100%) of the time, while the rest was composed of 12.7% of hunting (SD = 9.4; range: 0–75.2%) and 9.8% of commuting (SD = 7.4; range: 0–53.3%; Fig. S4).

Home range size and composition

Home range size varied significantly (mean = 6.6 km^2; range: 0.96–25.46; Fig. S5), with males having smaller home ranges than females. On the other hand, neither age, year nor date were related to the home range size (Table 1).

Table 1 Effect of individual and time parameters on barn owl home range size. Results from a linear-mixed model on 134 log-transformed home range sizes from 83 broods (set as random factor)

Parameter	Estimate ± SE	df	t-value	*p*
Intercept	2.028 ± 0.120	120.76	16.94	< 0.001
Sex[a]	−0.440 ± 0.102	68.77	−4.32	< 0.001
Date[b]	−0.032 ± 0.061	86.55	− 0.53	0.598
Year[a]	−0.166 ± 0.122	75.38	−1.37	0.176
Age[a]	−0.135 ± 0.117	128.90	−1.16	0.249

[a] Males minus females; 2017 minus 2016; older birds minus yearlings

[b] The Date parameter was scaled

Despite large inter-individual variations (Fig. 1), barn owl home ranges contained consistently and predominantly intensive agricultural fields (24.6% of cereals, 11.5% of intensive meadows, 10.4% of root vegetables and 7.1% of pastures). The forested areas were the second most represented habitat class (18.1% of forest and 5% of forest edges), followed by human-made constructions (10.9% of settlements and 8.4% of roads). Finally, extensively exploited areas were the rarest habitat class, with 4.1% of extensive meadows and 0.5% of wildflower strips. In addition to being the rarest habitat, wildflower strips were also absent in 21% of the home ranges (Fig. 1).

Home range selection

At the home range level, habitat selection revealed that barn owls incorporated in their home range some habitat types in disproportion compared to surrounding landscape (Fig. 2a). Intensive meadows and cereals were found in higher proportion in home ranges than in the nearby landscape, whereas settlements and forests were

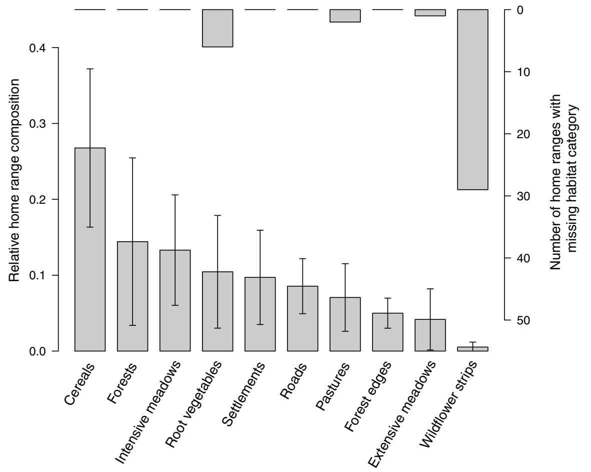


Fig. 1 Habitat composition of barn owl home ranges. For each of the 10 habitat categories, population mean and associated standard deviations are shown on the left axis, and the number of home ranges with missing habitat category on the right axis (134 home ranges in total). The habitats are ordered from the most to the least abundant

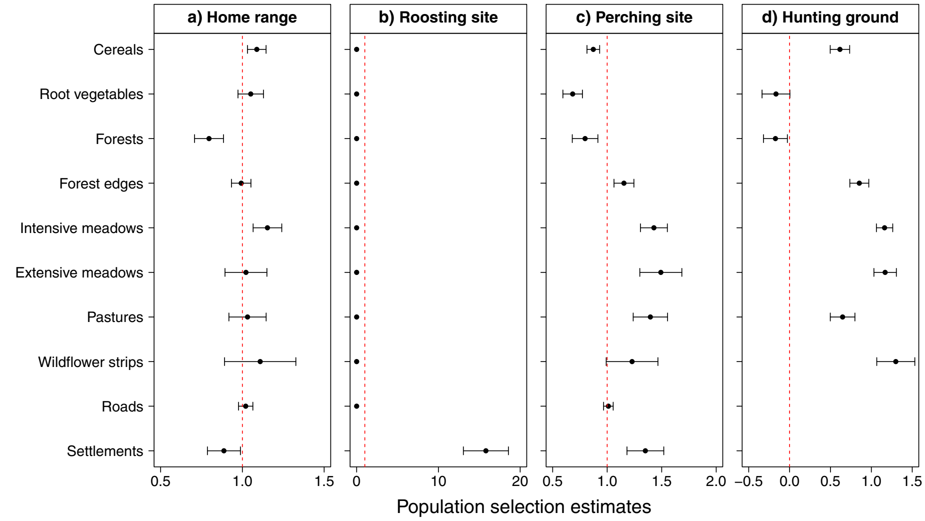


Fig. 2 Habitat selection population estimates. Home range composition, roosting and perching site selection analyses were computed following the Manly's third-order selection approach. Hunting ground selection followed the step-selection function (SSF) approach. Models were run for every individual and then averaged to obtain population estimates (mean and associated 95% confidence intervals are shown). Estimates on the right and left side of the dotted red line indicate, respectively, selected and avoided habitats

included in the home ranges in a smaller proportion than available. The selection ratios for the other habitat categories did not differ significantly from random use.

Roosting and perching site selection

Over the 915 daylight roosting events identified, 909 were located in barns or farms (468 in the nest box or in the nest box building, 441 in another building) and 6 were in forested areas, resulting in a clear selection pattern for settlements and avoidance of all 9 other habitat types (Fig. 2b). Roosting in natural habitats is thus an extremely rare event, concerning here 3 different females (out of 134 birds).

Overall habitat selection for night-time perching showed a clear pattern of habitat selection and avoidance (Fig. 2c). Among the habitats selected for perching, extensive meadows had the highest selection ratio, followed by intensive meadows, pastures, settlements and forest edges, while cereals, root vegetables and forests were avoided. Finally, roads and wildflower strips' selection ratios indicated a use according to their availability.

Hunting ground selection

The hunting SSF model revealed clear differences in selection ratios between the different habitat categories (Fig. 2d). Hunting owls avoided forests, and the root vegetables to a lesser extent, while selecting all six remaining habitat categories. Among the selected habitats, wildflower strips, extensive and intensive meadows were the most preferred ones, followed by forest edges, pastures and cereals. The scaled averaged estimates of the three movement parameters included in the models to increase the robustness of the habitat estimates were 0.04 for the cosine of the turning angle (SD = 0.15), −0.10 for the step length (SD = 0.39) and 0.21 for the log of the step length (SD = 0.53).

The three-dimensional NMDS model was associated with a stress value of 0.15, indicating a reliable representation of the coefficients of selection (Fig. S6). The first NMDS dimension contrasted between intensive meadows to root vegetables and forests, the second distinguished the forests, and the third one the root vegetables (Table S4). We tested if the similarity in habitat selection between individuals was related to the year and date of GPS installation, two proxies for structural and qualitative modifications of the landscape, and the owl sex and age, two parameters associated with individual investment and hunting experience. The permutation test showed a significant effect of the date ($r^2 = 0.24$, $p < 0.001$), whereas the year ($r^2 = 0.02$, $p = 0.19$), sex ($r^2 = 0.03$, $p = 0.12$) and age ($r^2 = 0.03$, $p = 0.11$) showed no significant relationship with hunting coefficient variations. The dimensions 2 and 3 of the NDMS encompassed most of the effect of the date (NMDS1 = -0.16, NMDS2 = 0.59, NMDS3 = -0.79), indicating higher root vegetable selection ratios at the end than at the beginning of the season, whereas the opposite was observed for forests (Fig. 3).

Commuting path analyses

The within habitat commuting PathSF model showed that all habitats considered were used for commuting, except for forest which was clearly avoided (Table 2). Considering

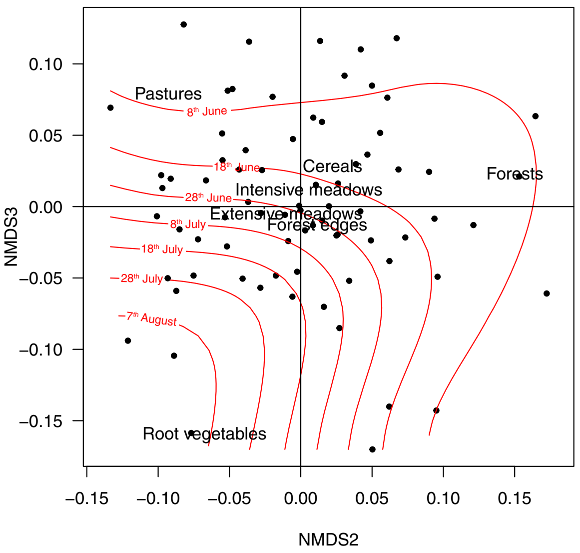


Fig. 3 Non-metric multi-dimensional scaling (NMDS) plot of hunting habitat selection estimates, each dot representing an individual. The effect of the date (in red) in the dimensions 2 and 3 (encompassing most of the date influence) is shown. Habitat categories are plotted for ease of understanding

all commuting flight types, owls covered a median distance of 447.7 m (range: 97.9–3676.1). The longest commuting flights were performed when returning to the nest, followed by the flights to leave it and the smallest distances covered were within the habitat (Fig. 4a, Table 3). When commuting, owls deviated 20.5 m (range: 0.1–991.2) on average from the most direct path. They deviated more from the straightest path when leaving the nest box than when they commuted in the habitat (Fig. 4b, Table 3). When commuting, owls flew at an average speed of 6.5 m/s (range: 3.4–13.4). They commuted the fastest to return to the nest box, followed by leaving it, and lastly within the habitat (Fig. 4c, Table 3).

Table 2 Commuting path selection. Using the path selection function approach (PathSF), selection ratios for each individual and habitat were extracted from a conditional logistic regression model including the five habitat categories listed and the burst as strata. Mean population selection estimates and associated 95% CI are shown, and the habitats are ordered from the most to the least preferred

Habitat	Selection ratio	Lower CI	Upper CI
Open intensive habitats	2.10	1.70	2.50
Roads	1.69	0.87	2.51
Open extensive habitats	1.52	1.04	2.01
Forest edges	1.05	0.24	1.85
Forests	−0.61	−1.19	−0.03

Discussion

In the context of preserving biodiversity in farmlands, our study provides a comprehensive breakdown of barn owl habitat selection during the reproductive season. The various behaviour-specific habitat analyses highlight the complementarity of this approach in understanding complex animal habitat preference and for proposing targeted conservation actions.

With an average size of 6.6 km^2, the home range sizes obtained in our study correspond to the ones previously described for barn owls in Europe [21, 25, 40, 41]. In this species, parental investment varies between sexes [42, 43], which is consistent with our finding that males had smaller home ranges than females. The bigger home range of females could be explained by double-brooded females which often desert their first brood to start a new one elsewhere with another mate [42, 44]. To find a new partner, females may prospect large areas, while their first male is still hunting close to their first nest.

Forested areas, commonly known to be avoided by barn owls, were under-represented in barn owl's home ranges, probably because its morphology (i.e. short tail and long wings) and hunting-on-the wing technique limits its use of closed habitats [21, 23]. Thus, home ranges contained mainly open habitats, with the most common ones - cereals and intensive meadows - being preferentially included (Fig. 2a). AES habitat categories were not selected at the home range level. Increasing the proportion of AES, the least represented habitat with low connectivity between each patch, in the home range likely implies the inclusion of the more abundant habitat categories.

Despite selection at the home range level being characterized by a preference for the most common habitats, behaviour-specific analyses revealed distinctive habitat use depending on the behavioural mode. During the day, barn owls roosted almost exclusively in buildings despite the apparent availability of natural sites (Fig. 2b). They might use the urban environment to shelter against adverse weather conditions, minimize the energy invested to thermoregulate and reduce the risk of predation or disturbance by competitors [45, 46].

During the night, barn owls preferred to perch in meadows, pastures, settlements and along forest edges (Fig. 2c). Perching habitat selection pattern was fairly similar to that of hunting, hinting at the use of the sit-and-wait hunting technique seen in many raptors [21, 47]. It may also reflect an opportunistic behaviour, in which resting or preening close to hunting grounds could offer the opportunity to capture a prey [48, 49]. In addition to the natural perching sites, barn owls also benefit from the fencing of pastures and artificial poles that are installed by farmers to attract raptors as pest-control agent [50].

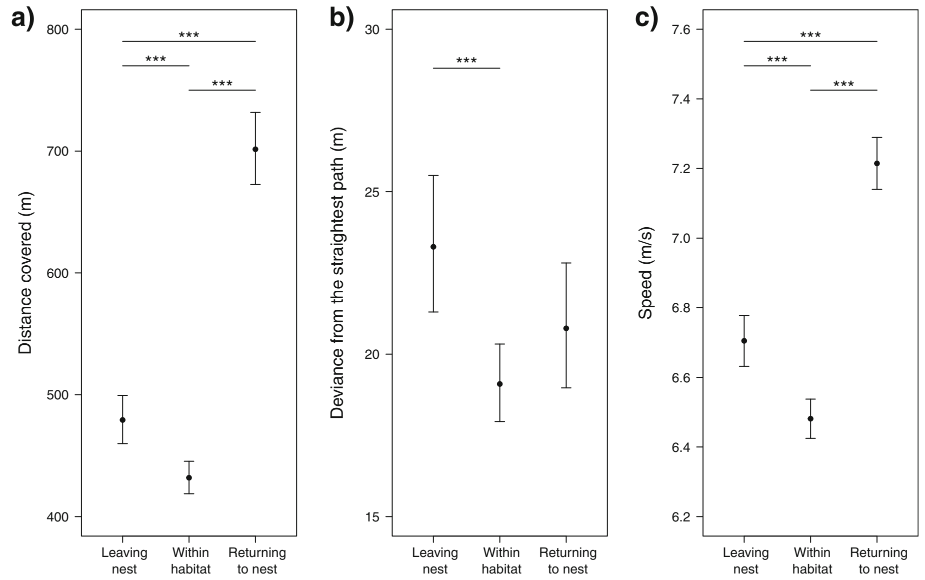


Fig. 4 Comparison of three type of commuting flights (leaving the nest, commuting within the habitat, and returning to the nest). Panel **a**) shows the distance covered, **b**) the deviance from the straightest path, and **c**) the flight speed. For each flight type, the mean and 95% confidence intervals are shown

For hunting, barn owls displayed a strikingly contrasted selection pattern, with habitats being either preferred or avoided but not neutral (i.e. used at the same frequency as availability; Fig. 2d). Surprisingly, most habitats were actually selected as hunting grounds, with a wide range of vegetation structure, prey abundance and agricultural regimes, reflecting the species' flexibility and adaptability. In a previous study, Arlettaz et al. (2010) showed a preference for cereals and intensive meadows (referred to as grassland in their study), arguing that vegetation structure was more important than prey availability. Our results confirm a selection for these habitats as hunting grounds, but also highlight the importance of extensive meadows and wildflower strips, the rarest but most preferred hunting habitats. The habitats selected for hunting differ strongly in vegetation height, and we found no seasonal selection differences in habitats with large fluctuations in vegetation structure throughout the year. Therefore, we could not find a limitation of habitat use based on vegetation structure as previously proposed [7, 51]. Further research should investigate the interconnected effects of vegetation structure and prey density on hunting ground selection and success, while accounting for individual specific foraging strategies (on the wing or perched). In addition, as barn owls display a plumage colour polymorphism [23], upcoming studies should investigate morph-specific habitat preferences and foraging strategies, specifically in relation to night illumination [52].

Table 3 Difference between the three types of commuting – leaving (L) the nestbox, returning (R) to it and within (W) the habitat – in the distance covered, deviance from the straightest path and flight speed. Results from linear-mixed models including 12,503 tracks from 134 barn owls (owl identity set as random factor). The distance covered and the deviance from the straightest path were log-transformed

Parameter	Estimate ± SE	df	t-value	*p*
Distance covered				
L - W	−0.104 ± 0.017	12,470	−6.20	< 0.001
L - R	−0.381 ± 0.022	12,412	17.30	< 0.001
W - R	−0.485 ± 0.0174	12,461	27.93	< 0.001
Deviance from the straightest path				
L - W	−0.199 ± 0.039	12,490	−5.02	< 0.001
L - R	−0.114 ± 0.052	12,439	−2.18	0.078
W - R	−0.086 ± 0.041	12,484	2.09	0.101
Speed				
L - W	−0.224 ± 0.028	12,468	−7.83	< 0.001
L - R	−0.510 ± 0.037	12,411	13.62	< 0.001
W - R	−0.733 ± 0.029	12,454	24.83	< 0.001

Similarly to the other behavioural modes, commuting tracks bypassed the forested areas (Table 2). Flying over such tall structures as forest would possibly require a larger energetic investment for this usually low-flying bird [21]. Commuting tracks followed nearly straight paths and are hence optimised to reach their destination at high speed as directly as possible (Fig. 4). Since the flights to leave the nest box are shorter than those to return to it, owls might gradually move away from their nest box during the hunt. As central place foragers carrying one prey per nest visit, it would be advantageous for the owls to optimize their energy expenditure by starting to hunt close to the nest [53, 54]. Although most commuting flights were almost straight, some specific tracks deviated considerably from the shortest route (up to 991 m of difference), possibly due to fine-scale environmental or habitat structure variations. Avoiding adverse conditions such as strong head-winds or taking advantage of potential uplifts along tall structures could justify taking a longer route while optimizing energy expenditure [55].

Conclusions

This study highlights the need of behaviour-specific analyses to understand complex animal habitat preferences. The combination of the results unveils the barn owl as a generalist and opportunistic bird, with plastic behaviour to exploit a variety of open habitats in a farmland landscape. In comparison with a previous study [51], our results showed that barn owls select AES habitats, such as wildflower strips and extensive meadows, as hunting grounds. This supports the importance of such schemes to restore and maintain functional trophic chains in farmland, and stresses the need to promote such measures that are still rare and scattered. The quality of these areas dedicated to biodiversity could also be improved by increasing the connectivity between these plots [56, 57]. In addition, their use by raptors could be enhanced through the installation of artificial poles in dense vegetation to favour the use of the sit-and-wait hunting technique [58, 59]. Future analyses should investigate the profitability of AES for farmland raptors, by translating AES availability and use into fitness benefits. Finally, our work demonstrates the importance of addressing habitat selection on a behaviour-specific perspective to account for the complex animal habitat selection patterns when proposing appropriate conservation plans.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-021-00258-6.

Additional file 1: Table S1. For each habitat category are given the source of the data, and the object with the associated buffer used for creating the layers. **Table S2.** Correspondence between habitat classification and official agri-environment schemes (AES) categories. **Table S3.** Number of barn owl individuals included in habitat selection models. **Table S4**. Correspondence between habitat categories and the three dimensions of the non-metric multi-dimensional scaling (NMDS) performed on hunting selection estimates. **Fig. S1.** Step length and turning angle distributions for the perching, hunting and commuting behaviours. **Fig. S2.** Relation between hunting and commuting flight speeds and the behavioural event duration. **Fig. S3.** Distribution of night activity period duration, defined as the time between two daylight roosting events. **Fig. S4.** Proportion of activity time per night spent perching, hunting or commuting. **Fig. S5.** Home range size in relation to barn owl sex. **Fig. S6.** Non-metric multi-dimensional scaling (NMDS) model parametrization.

Acknowledgements

We thank C. Gémard, E. Mayor, S. Zurkinden, C. Plancherel, R. Sartori, C. Sahli, M. Déturche, M. Chèvre, J. Ehinger and N. Apolloni for their help in collecting field data, P. Béziers, L.M.San-Jose and R. Spaar for their support in the early development of the project.

Authors' contributions

All authors designed the project, A. Roulin and B. Almasi funded the research. R. Séchaud, K. Schalcher, A.P.Machado and C. Massa collected data. R. Séchaud and K. Schalcher analysed data. R. Séchaud wrote the manuscript, with significant contributions of all co-authors. The authors read and approved the final manuscript.

Funding

This study was financially supported by the Swiss National Science Foundation (grants no. 31003A_173178, to Alexandre Roulin) and Swiss Confederation (grants no. 2015.0788, to Carolina Massa).

Availability of data and materials

The GPS datasets generated and analysed during the current study are available in Movebank (www.movebank.org), under the project named "Barn owl (*Tyto alba*)" (ID 231741797). The habitats maps produced during the current 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]Department of Ecology and Evolution, University of Lausanne, Building Biophore, CH-1015 Lausanne, Switzerland. [2]Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland. [3]Instituto de Investigación e Ingeniería Ambiental, Laboratorio de Ecología de Enfermedades Transmitidas por Vectores, Universidad Nacional de San Martín, 25 de Mayo, 1650 San Martín, Buenos Aires, Argentina. [4]Inmunova S.A., 25 de Mayo, 1650 San Martín, Buenos Aires, Argentina. [5]Department of Migration, Max Planck Institute of Animal Behaviour, Am Obstberg 1, 78315 Radolfzell, Germany. [6]Department of Biology, University of Konstanz, Universitätsstraße 10, 78464 Constance, Germany.

Received: 19 January 2021 Accepted: 31 March 2021

References

1. Green RE, Cornell SJ, Scharlemann JP, Balmford A. Farming and the fate of wild nature. Science (80-). 2005;307:550–5 [cited 2018 Feb 8]. Available from: http://www.ncbi.nlm.nih.gov/pubmed/11303102.
2. 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. 2009;91:22–46 [cited 2018 Feb 8]. Available from: https://www.sciencedirect.com/science/article/pii/S0301479709002448.

3. Donald PF, Green RE, Heath MF. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc R Soc Lond Ser B Biol Sci. 2001; 268:25–9 [cited 2020 Jun 24]. Available from: https://royalsocietypublishing.org/doi/10.1098/rspb.2000.1325.
4. Robinson RA, Sutherland WJ. Post-war changes in arable farming and biodiversity in Great Britain. J Appl Ecol. 2002;39:157–76[cited 2020 Mar 18]. Available from. https://doi.org/10.1046/j.1365-2664.2002.00695.x.
5. Kremen C, Williams NM, Thorp RW. Crop pollination from native bees at risk from agricultural intensification. Proc Natl Acad Sci U S A. 2002;99:16812–6 [cited 2020 Jun 24]. Available from: http://www.ncbi.nlm.nih.gov/pubmed/12486221.
6. Kleijn D, Baquero RA, Clough Y, Díaz M, Esteban J, Fernández F, et al. Mixed biodiversity benefits of Agri-environment schemes in five European countries. Ecol Lett. 2006;9:243–54[cited 2018 Feb 8]. Available from. https://doi.org/10.1111/j.1461-0248.2005.00869.x.
7. Aschwanden J, Birrer S, Jenni L. Are ecological compensation areas attractive hunting sites for common kestrels (*Falco tinnuculus*) and long-eared owls (*Asio otus*)? J Ornithol. 2005;146(3):279–86. https://doi.org/10.1007/s10336-005-0090-9.
8. Zingg S, Ritschard E, Arlettaz R, Humbert JY. Increasing the proportion and quality of land under Agri-environment schemes promotes birds and butterflies at the landscape scale. Biol Conserv. 2019;231:39–48. https://doi.org/10.1016/j.biocon.2018.12.022.
9. Wade MR, Gurr GM, Wratten SD. Ecological restoration of farmland: Progress and prospects. Philos Trans R Soc B Biol. 2008:831–47 [cited 2020 Aug 31]. Available from: https://royalsocietypublishing.org/doi/abs/10.1098/rstb.2007.2186.
10. Roever CL, Beyer HL, Chase MJ, van Aarde RJ. The pitfalls of ignoring behaviour when quantifying habitat selection. Roura-Pascual N, editor. Divers Distrib. 2014;20:322–33[cited 2020 Jul 29]. Available from. https://doi.org/10.1111/ddi.12164.
11. Dussault C, Quellet JP, Courtois R, Huot J, Breton L, Jolicoeur H. Linking moose habitat selection to limiting factors. Ecography (Cop). 2005;28:619–28 [cited 2020 Oct 28]. Available from: https://onlinelibrary.wiley.com/doi/full/10.1111/j.2005.0906-7590.04263.x.
12. Smith LM, Hupp JW, Ratti JT. Habitat use and home range of gray partridge in eastern South Dakota. J Wildl Manag. 1982;46:580–7 [cited 2018 Feb 8]. Available from: http://www.jstor.org/stable/3808548?origin=crossref.
13. Stamps JA, Davis JM. Adaptive effects of natal experience on habitat selection by dispersers. Anim Behav. 2006;72:1279–89 [cited 2018 Feb 8]. Available from: https://www.sciencedirect.com/science/article/pii/S0003347206002855.
14. Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP. Habitat selection at multiple scales. Ecoscience. 2009;16:238–47 [cited 2017 Feb 10]. Available from: https://pubag.nal.usda.gov/pubag/article.xhtml?id=1267421.
15. McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA. Multi-scale habitat selection modeling: a review and outlook. Landsc Ecol. 2016;31:1161–75 [cited 2020 Jul 8]. Available from: https://link.springer.com/article/10.1007/s10980-016-0374-x.
16. Fauchald P, Tveraa T. Using fisrt-passage time in the analysis of area-restricted search and habitat selection. Ecology. 2003;84:282–8 [cited 2018 Feb 8]. Available from: http://onlinelibrary.wiley.com/doi/10.1890/0012-9658(2003)084%5B0282:UFPTIT%5D2.0.CO;2/abstract.
17. Jonsen I, Myers R, James M. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Mar Ecol Prog Ser. 2007;337:255–64 [cited 2020 Aug 31]. Available from: http://www.int-res.com/abstracts/meps/v337/p255-264/.
18. Garriga J, Palmer JRB, Oltra A, Bartumeus F. Expectation-maximization binary clustering for Behavioural annotation. PLoS One. 2016;11:e0151984 [cited 2018 Jan 2]. Available from: http://journals.plos.org/plosone/article/file?id=10.1371/journal.pone.0151984&type=printable.
19. Suraci JP, Frank LG, Oriol-Cotterill A, Ekwanga S, Williams TM, Wilmers CC. Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. Ecology. 2019;100:e02644 [cited 2020 Aug 31]. Available from: https://onlinelibrary.wiley.com/doi/abs/10.1002/ecy.2644.
20. De Bruijn O. Population ecology and conservation of the barn owl *Tyto alba* in farmland habitats in liemers and achterhoek (the Netherlands). ARDEA. 1994:1–109 [cited 2018 Feb 8]. Available from: http://www.avibirds.com/pdf/K/Kerkuil3.pdf.
21. Taylor I. Barn owls: predator-prey relationships and conservation: Cambridge University Press; 1994.
22. 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[cited 2014 Dec 20]. Available from:. https://doi.org/10.1007/s10336-010-0579-8.
23. Roulin A. *Tyto alba* barn owl. BWP Updat. 2002;4:115–38 [cited 2020 Jun 29]. Available from: https://serval.unil.ch/notice/serval:BIB_2CBA948E4914.
24. QGIS Development Team, QGIS. QGIS geographic information system; 2017. Open Source Geospatial Foundation.
25. 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(1):161–71. https://doi.org/10.1016/j.yhbeh.2013.03.001.
26. R Core Team. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing; 2018. URL https://www.R-project.org/
27. Worton BJ. Kernel methods for estimating the utilization distribution in home-range studies. Ecology. 1989;70:164–8[cited 2018 Jan 2]. Available from. https://doi.org/10.2307/1938423.
28. Calabrese JM, Fleming CH, Gurarie E. Ctmm : an R package for analyzing animal relocation data as a continuous-time stochastic process. Freckleton R, editor. Methods Ecol Evol. 2016;7:1124–32[cited 2018 Jan 2]. Available from. https://doi.org/10.1111/2041-210X.12559.
29. Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology. 2015;96:1182–8[cited 2017 Jan 16]Available from:. https://doi.org/10.1890/14-2010.1.
30. Kuznetsova A, Brockhoff PB, Christensen RHB. lmerTest package: tests in linear mixed effects models. J Stat Softw. 2017;82:1–26 [cited 2020 Dec 3]. Available from: https://www.jstatsoft.org/index.php/jss/article/view/v082i13/v82i13.pdf.
31. Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. Resource selection by animals : statistical design and analysis for field studies: Kluwer Academic Publishers; 2002.
32. Calenge C. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model. 2006;197(3-4):516–9. https://doi.org/10.1016/j.ecolmodel.2006.03.017.
33. Thurfjell H, Ciuti S, Boyce MS. Applications of step-selection functions in ecology and conservation. Mov Ecol. 2014;2:4 [cited 2019 May 8]. Available from: https://movementecologyjournal.biomedcentral.com/articles/10.1186/2051-3933-2-4.
34. Signer J, Fieberg J, Avgar T. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecol Evol. 2019;9:880–90[cited 2020 Jul 21]. Available from. https://doi.org/10.1002/ece3.4823.
35. Duchesne T, Fortin D, Rivest L-P. Equivalence between step selection functions and biased correlated random walks for statistical inference on animal movement. Petit O, editor. PLoS One. 2015;10:e0122947[cited 2020 Jul 21]. Available from. https://doi.org/10.1371/journal.pone.0122947.
36. Avgar T, Potts JR, Lewis MA, Boyce MS. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Börger L, editor. Methods Ecol Evol. 2016;7:619–30[cited 2019 May 8]. Available from. https://doi.org/10.1111/2041-210X.12528.
37. Minchin PR. An evaluation of the relative robustness of techniques for ecological ordination. Theory Model Veg Sci. 1987:89–107[cited 2020 Aug 5]. Available from:. https://doi.org/10.1007/978-94-009-4061-1_9.
38. Dixon P. VEGAN, a package of R functions for community ecology. J Veg Sci. 2003:927–30 [cited 2020 Aug 5]. Available from: https://onlinelibrary.wiley.com/doi/full/10.1111/j.1654-1103.2003.tb02228.x.
39. Cushman SA, Lewis JS. Movement behavior explains genetic differentiation in American black bears. Landsc Ecol. 2010;25:1613–25[cited 2020 Jul 31]. Available from:. https://doi.org/10.1007/s10980-010-9534-6.
40. Brandt T, Seebass C. In: Wiesbaden, editor. Die Schleiereule: AULA-Verlag; 1994. [cited 2020 Nov 25]. Available from: https://www.amazon.de/Die-Schleiereule-heimlichen-Kulturfolgers-AULA-Verlag/dp/3891045417.
41. Michelat D, Giraudoux P. Dimension du domaine vital de la chouette effraie *Tyto alba* pendant la nidification. Alauda. 1991;59:137–42.
42. Roulin A. Offspring desertion by double-brooded female barn owls (Tyto Alba). Auk. 2002;119(2):515–9. https://doi.org/10.1093/auk/119.2.515.

43. Roulin A. Nonrandom pairing by male barn owls (Tyto alba) with respect to a female plumage trait. Behav Ecol. 1999;10(6):688–95. https://doi.org/10.1093/beheco/10.6.688.
44. Béziers P, Roulin A. Double brooding and offspring desertion in the barn owl *Tyto alba*. J Avian Biol. 2016;47(2):235–44. https://doi.org/10.1111/jav.00800.
45. Lausen CL, Barclay RMR. Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. J Mammal. 2006;87:362–70 [cited 2020 Sep 3]. Available from: https://academic.oup.com/jmammal/article-lookup/doi/10.1644/05-MAMM-A-127R1.1.
46. Blair R. The effects of urban sprawl on birds at multiple levels of biological organization. Ecol Soc Soc. 2004;9(4). https://www.jstor.org/stable/26267695. Accessed 9 Apr 2021.
47. Jaksic FM, Carothers JH. Ecological, morphological, and bioenergetic correlates of hunting mode in hawks and owls. Ornis Scand. 1985;16(3):165–72. https://doi.org/10.2307/3676627.
48. Kullberg C. Strategy of the pygmy owl while hunting avian and mammalian prey. Ornis Fenn. 1995;72:72–8.
49. Hopcraft JGC, Sinclair ARE, Packer C. Planning for success: Serengeti lions seek prey accessibility rather than abundance. J Anim Ecol. 2005;74:559–66[cited 2021 Mar 10]. Available from. https://doi.org/10.1111/j.1365-2656.2005.00955.x.
50. Kross SM, Bourbour RP, Martinico BL. Agricultural land use, barn owl diet, and vertebrate pest control implications. Agric Ecosyst Environ. 2016;223:167–74 [cited 2016 Mar 24]. Available from: http://www.sciencedirect.com/science/article/pii/S0167880916301293.
51. 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[cited 2016 Mar 25]. Available from:. https://doi.org/10.1007/s10336-009-0485-0.
52. San-Jose LM, Séchaud R, Schalcher K, Judes C, Questiaux A, Oliveira-Xavier A, et al. Differential fitness effects of moonlight on plumage colour morphs in barn owls. Nat Ecol Evol. 2019;3:1331–40[cited 2020 Jul 24]. Available from. https://doi.org/10.1038/s41559-019-0967-2.
53. Patenaude-Monette M, Bélisle M, Giroux J-F. Balancing energy budget in a central-place forager: which habitat to select in a heterogeneous environment? Sears M, editor. PLoS One. 2014;9:e102162[cited 2021 Mar 10]. Available from:. https://doi.org/10.1371/journal.pone.0102162.
54. Charnov EL. Optimal foraging, the marginal value theorem. Theor Popul Biol. 1976;9(2):129–36. https://doi.org/10.1016/0040-5809(76)90040-X.
55. Péron G, Fleming CH, Duriez O, Fluhr J, Itty C, Lambertucci S, et al. The energy landscape predicts flight height and wind turbine collision hazard in three species of large soaring raptor. Bauer S, editor. J Appl Ecol. 2017;54:1895–906[cited 2020 Aug 9]. Available from:. https://doi.org/10.1111/1365-2664.12909.
56. Frey-Ehrenbold A, Bontadina F, Arlettaz R, Obrist MK. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. Pocock M, editor. J Appl Ecol. 2013;50:252–61[cited 2021 Mar 10]. Available from:. https://doi.org/10.1111/1365-2664.12034.
57. Aviron S, Lalechère E, Duflot R, Parisey N, Poggi S. Connectivity of cropped vs. semi-natural habitats mediates biodiversity: a case study of carabid beetles communities. Agric Ecosyst Environ. 2018;268:34–43.
58. Kay BJ, Twigg LE, Korn TJ, Nicol HI. The use of artificial perches to increase predation on house mice (Mus domesticus) by raptors. Wildl Res. 1994;21:739–43 [cited 2021 Mar 10]. Available from: https://www.publish.csiro.au/wr/wr9940095.
59. Widen P. Habitat quality for raptors: a field experiment. J Avian Biol JSTOR. 1994;25:219.

Publisher's Note

Chapter 1 – Supplementary information

Table S1. For each habitat category are given the source of the data, and the object with the associated buffer used for creating the layers.

Habitat category	Source	Object	Buffer
Cereals	Field monitoring	-	-
Root vegetables	Field monitoring	-	-
Pastures	Field monitoring	-	-
Intensive meadows	Field monitoring	-	-
Extensive meadows	Field monitoring	-	-
Wildflower strips	Field monitoring	-	-
Forests	SwissTLM^{3D}	TLM_BODENBEDECKUNG	
		OBJEKTART = Wald	-
		OBJEKTART = Wald offen	-
		OBJEKTART = Gebueschwald	-
Forest edges	SwissTLM^{3D}	Buffer around "Forests" layer	10 m
Roads	SwissTLM^{3D}	TLM_STRASSE	
		OBJEKTART = Autobahn	25 m
		OBJEKTART = Autostrasse	15 m
		OBJEKTART = 10m Strasse	10 m
		OBJEKTART = 8m Strasse	8 m
		OBJEKTART = 6m Strasse	6 m
		OBJEKTART = 4m Strasse	4 m
		OBJEKTART = 3m Strasse	3 m
		OBJEKTART = 2m Weg	2 m
		OBJEKTART = 1m Weg	1 m
Settlements	SwissTLM^{3D}	TLM_GEBAEUDE_FOOTPRINT	
		OBJEKTART = all	20 m

Table S2. Correspondence between habitat classification and official agri-environment schemes (AES) categories. The official AES census performed by the canton Vaud in 2017 was compared to 24 corresponding vegetation maps mapped in this study (selected based on their location and year of mapping). The AES category identifiers correspond to the ones defined by the Federal Office for Agriculture (FOAG): 556 = Floral fallow; 557 = Rotational fallow; 559 = Extensive herbaceous strips; 611 = Extensive meadows; 612 = Low intensity meadows; 617 = Extensive pastures; 852 = Hedges and copses. Percentage of correspondence are indicated with the number of matching parcels in brackets.

	AES category identifiers							**non-AES**	**Total**
	556	**557**	**559**	**611**	**612**	**617**	**852**		
Wildflower strips	70.23% (92)	26.72% (35)	2.29% (3)	0.76% (1)	0	0	0	0	131
Extensive meadows	0.17% (1)	0.50% (3)	0.17% (1)	93.68% (563)	1.83% (11)	1.83% (11)	1.32% (8)	0.50% (3)	601
Intensive meadows	0	0	0	5.44% (102)	5.39% (101)	0.96% (18)	0	88.21% (1653)	1874
Pastures	0	0	0	8.96% (82)	0	18.80% (172)	1.09% (10)	71.15% (651)	915

Table S3. Number of barn owl individuals included in habitat selection models. For each analysis, poorly estimated coefficients (because the habitat category was absent or too rare) were removed from the models to avoid misestimating the other habitat selection estimates. In total, 134 barn owls were included in the study.

Category	Home range	Roosting site	Perching site	Hunting ground
Cereals	134	134	134	134
Root vegetables	122	128	127	114
Forests	134	134	134	117
Forest edges	134	134	134	131
Intensive meadows	134	134	134	132
Extensive meadows	131	133	132	115
Pastures	132	132	132	118
Wildflower strips	115	104	104	62
Roads	134	134	134	-
Settlements	134	134	134	-

Table S4. Correspondence between habitat categories and the three dimensions of the non-metric multi-dimensional scaling (NMDS) performed on hunting selection estimates.

Habitat	**NMDS 1**	**NMDS 2**	**NMDS 3**
Cereals	-0.033	-0.023	-0.028
Root vegetables	0.146	0.070	0.160
Forests	0.138	-0.150	-0.021
Forest edges	-0.062	-0.011	0.014
Intensive meadows	-0.114	-0.006	-0.012
Extensive meadows	-0.005	0.010	0.004
Pastures	0.092	0.092	-0.081

Fig. S1. Step length and turning angle distributions for the perching, hunting and commuting behaviours. The step length is in meters and the turning angle in radians, with a time interval between each location of 10 seconds.

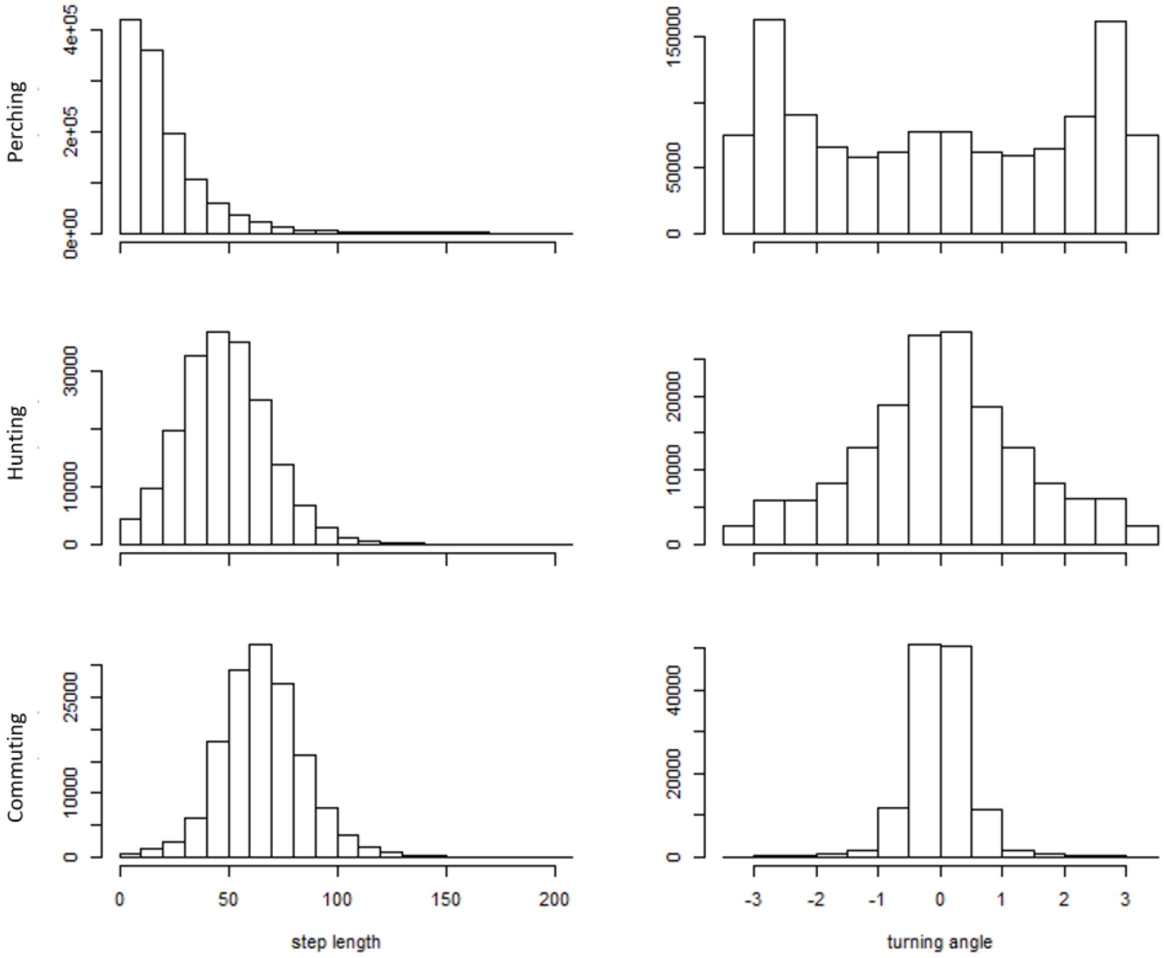


Fig. S2. Relation between a) hunting and b) commuting flight speeds and the behavioural event duration.

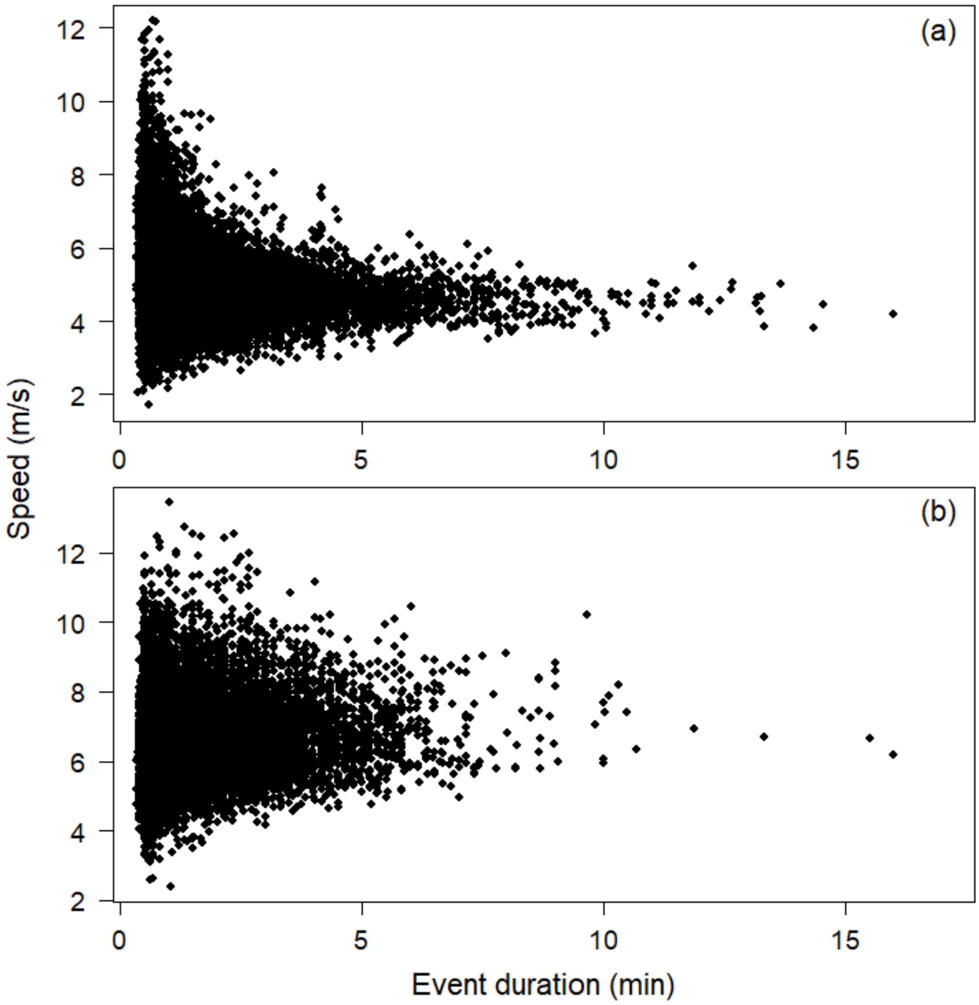


Fig. S3. Distribution of night activity period duration, defined as the time between two daylight roosting events.

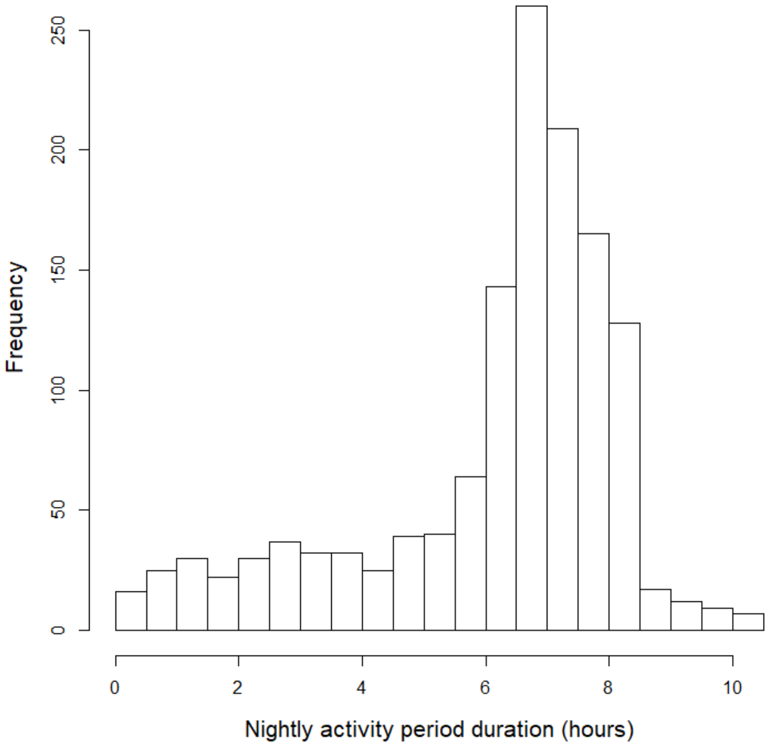


Fig. S4. Proportion of activity time per night spent perching, hunting or commuting.

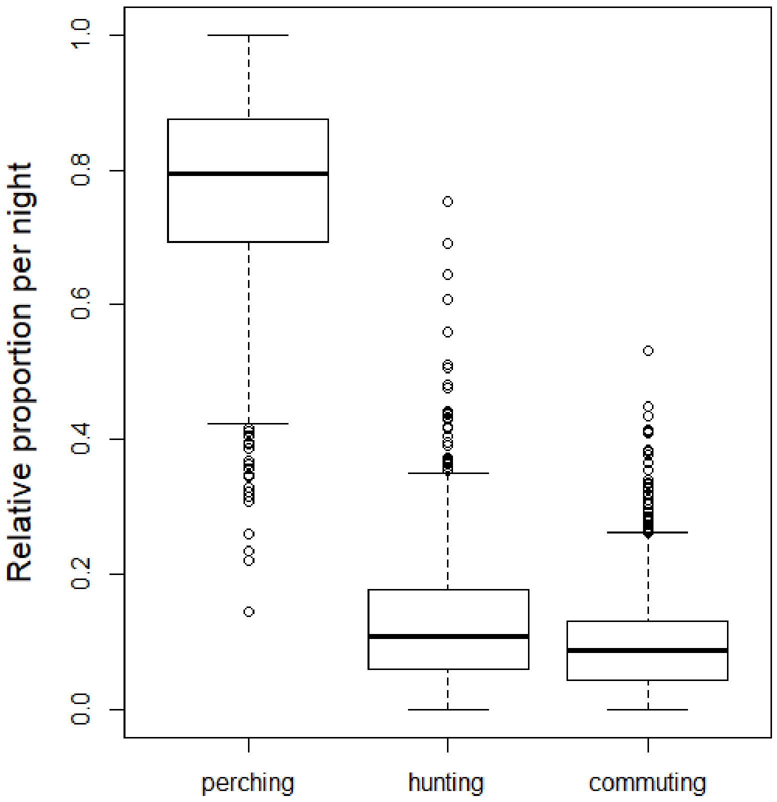


Fig. S5. Home range size in relation to barn owl sex.

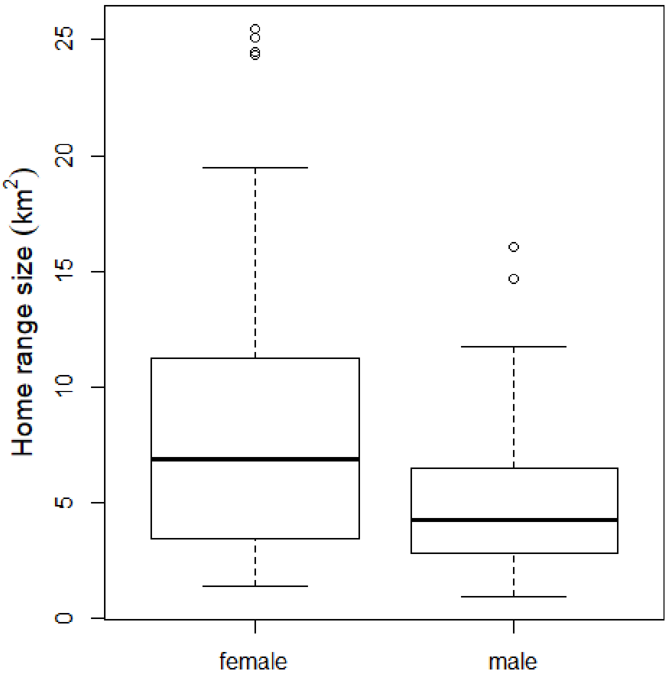
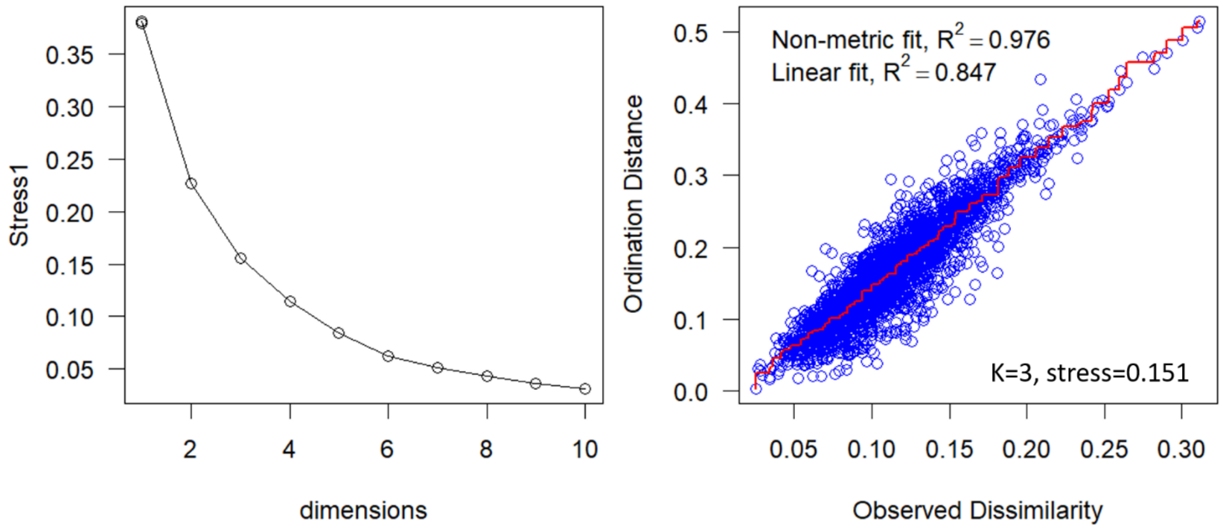


Fig. S6. Non-metric multi-dimensional scaling (NMDS) model parametrization. NMDS was built in three dimensions, resulting in a stress value of 0.15 and an acceptable fit.



Chapter 2

Home range size and habitat quality affect breeding success but not parental investment in barn owl males

Robin Séchaud[1], Kim Schalcher[1], Bettina Almasi[2], Andrea Romano[3†] and Alexandre Roulin[1†]

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

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

[3] Department of Environmental Science and Policy, University of Milan, Milan, Italy.

[†] co-senior authors

Chapter Status:

In preparation. It will be submitted soon in Journal of Animal Ecology.

Author contributions:

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

Abstract

1. Life-history theory predicts that parents should balance their limited resources to maximize their lifetime fitness. In particular, when the fitness value of current progeny is lower than that gained by producing offspring in the future, parents should prudently limit their investment in current reproduction, possibly resulting in breeding failure or brood reduction, while improving self-maintenance and reproducing in the future. Such individual trade-offs are expected to be mediated by the environmental conditions to which individuals are exposed.

2. We investigated whether habitat quality, as gauged by the proportion of suitable hunting habitats in the surrounding of the nest, affects home range size, parental investment and reproductive success in barn owl (*Tyto alba*) males. Specifically, we tested whether males breeding in low-quality habitats increased their parental effort to successfully complete offspring rearing or limited their investment by paying a fitness cost while saving energies for the future.

3. We deployed a large number of males with GPS and collected information on habitat quality and home range size. We also recorded food provisioning rate to the brood, nighty distance covered, and body mass variation, as proxies of parental investment, and nestlings' growth and survival, as proxies of reproductive success. We finally examined the reproductive success in the breeding season following the one under investigation.

4. Males living in high-quality habitats exploited smaller home ranges compared to individuals whose nest was located in fragmented habitats where prey were scattered. Males living in large home ranges fed their brood less frequently, although they covered longer nightly distance, resulting in a slower growth of late-hatched nestlings and ultimately in a smaller fledging success. However, their body mass change during the period of offspring rearing was similar to that of males living in small home ranges, as well as they had the same likelihood of reproducing than the other males in the next breeding season.

5. Therefore, males exposed to limiting ecological conditions did not increase their parental investment to compensate for the lower prey abundance near the nest, and, by favouring brood reduction, traded-off their current fitness versus future breeding opportunities.

Key words

Feeding rate, Habitat quality, Parental investment, Reproductive success, Trade-off

Introduction

A central issue in life-history theory concerns how parents optimally balance their limited resources in order to maximize their lifetime fitness (Roff, Mostowy, & Fairbairn, 2002; Stearns, 1992). In species with altricial progeny, rearing offspring is among the most energetically demanding activity for the parents (Drent & Daan, 1980; Harshman & Zera, 2007; Lack, 1947; Reznick, 1985). Parental investment in the current reproduction is therefore expected to carry high costs, which can result in trade-offs against parental survival (e.g. Cox et al., 2010; Dijkstra, Daan, & Tinbergen, 1990; Marshall & Sinclair, 2010) and future reproduction (Candolin, 1998; Merilä & Fry, 1998; Nilsson & Svenssonn, 1996; Perrins, 1965; Rivalan et al., 2005; Walker, Gurven, Burger, & Hamilton, 2008). It is generally recognized that when the reproductive effort in one breeding event results in a considerable loss in future fitness, via a decrease in survival and/or a reduced fecundity, the optimal parental investment is smaller than the amount that would maximize offspring production in such a reproductive event (Charnov & Krebs, 1974; Williams, 1966). In practice, whenever the cost of a reduced annual fitness would be overcompensated by a larger increase in future fitness it can be advantageous for the parents to prudently limit their investment in current reproduction, thus resulting in breeding failure or brood reduction (Ricklefs, 1977; Williams, 1966).

The successful completion of offspring rearing may depend on individual quality but also on the environmental conditions experienced by both the parents and the offspring. It is well-known that parents are usually limited by food availability (Martin, 1987), which is typically related to the quality and the structure of the environment where the breeding occurs, which may considerably constrain the investment in the current offspring (Kaiser, Scott Sillett, Risk, & Webster, 2015; Kouba, Bartoš, Sindelář, & St'astny, 2017; Santangeli, Hakkarainen, Laaksonen, & Korpimäki, 2012). In particular, when habitat is degraded and fragmented, available resources become increasingly scattered and isolated, thus forcing individuals to maintain larger home ranges (Redpath, 1995) and to forage at increasing distances from their breeding site (Bruun & Smith, 2003; Frey-Roos, Brodmann, & Reyer, 1995). There is indeed a wide literature linking habitat quality and individual/group home range size, both in primary consumers (Saïd et al., 2009; Van Beest, Rivrud, Loe, Milner, & Mysterud, 2011) and predators (Hakkarainen, Koivunen, & Korpimäki, 1997; Kittle et al., 2015; Kouba et al., 2017; Mirski & Väli, 2021; Redpath, 1995; Santangeli et al., 2012), as well as that an increase in home range size results in lower provisioning rate to the offspring (Bruun & Smith, 2003; Frey-Roos et al., 1995), longer distances covered (Bruun & Smith, 2003; Hakkarainen et al., 1997; Trembley, Thomas, Blondel, Perret, & Lambrechts, 2004) and larger energetic costs to the parents (Turcotte & Desrochers, 2003). The ultimate consequence may be a decrease in current reproductive success (Hinam & Clair, 2008; Hinsley, Rothery, & Bellamy, 1999) or survival (Daan, Deerenberg, & Dijkstra, 1996). Under limiting ecological conditions, parents have therefore to decide whether compensating through an increase in their reproductive effort in order to successfully complete offspring rearing at the expense of their future reproduction (Budden & Beissinger, 2009; Slagsvold, Sandvik, Rofstad, Lorentsen, & Husby, 1984; Tripet, Richner, & Tripet, 1997) or prudently limiting their investment, possibly resulting in a decrease in their current fitness, in order to improve self-maintenance and gain future reproductive chances (Bókony et al., 2009; Drent & Daan, 1980). However, there is still a dearth of studies investigating how habitat quality can affect individual decisions on the amount of investment to be devoted in parental care, and how it can mediate individual trade-offs (see Caro, Griffin, Hinde, & West, 2016; Ghalambor & Martin, 2001; McGinley, Temme, & Geber, 1987) .

To examine how parental investment in offspring rearing, reproductive success and future reproduction are affected by habitat quality, we performed a GPS tracking study on a large sample of male barn owls (*Tyto alba*), recording home range size and habitat characteristics. This species is a farmland nocturnal raptor of medium size, that preys almost exclusively on small mammals (Romano, Séchaud, & Roulin, 2020; Roulin, 2004). It breeds in farms and barns, and hunts preferentially in extensive open habitats, such as meadows and wildflower strips (Arlettaz, Krähenbühl, Almasi, Roulin, & Schaub, 2010; Castañeda, Huysman, & Johnson, 2021; Hindmarch, Elliott, Mccann, & Levesque, 2017; Séchaud et al., 2021). However, it can also exploit more intensive habitats, like grasslands and cereal crops, but show a strong avoidance for forests and urbanized areas (Castañeda et al., 2021; Hindmarch et al., 2017; Séchaud et al., 2021). The vast majority of food delivered to the altricial offspring is provided by the male, especially from the second week after hatching to the moment of fledging (Roulin, Ducrest, & Dijkstra, 1999), whereas females even sometimes leave their clutch to start a second one elsewhere (Béziers & Roulin, 2016).

Here, we aimed at investigating how habitat use and home range size, which is a proxy of habitat quality, affect male hunting behaviour and parental investment in terms of food provisioning to the nestlings, nightly distance covered and body mass variation during the rearing period, and how such a parental effort translates into offspring pre-fledging survival and quality, as well as into future reproduction. In particular, we predicted that home range size should decrease at increasing proportion of the main barn owl's hunting habitats surrounding individual nests, as males should increase their ranging behaviour if suitable habitats are less abundant in its proximity (Laaksonen, Hakkarainen, & Korpimäki, 2004; Redpath, 1995; Santangeli et al., 2012). In addition, male food provisioning rate should increase at decreasing home range size, while the opposite should be the case for nightly distance covered. In practice, males maintaining larger home ranges should pay larger costs, in terms of reduction in body mass and body condition (D. M. Bryant, 1988; Dijkstra et al., 1990; Merilä & Wiggins, 1997), than those living in high-quality habitats to provide the amount of food enough to successfully accomplish the nestlings rearing. We thus finally tested two competing hypothesis about male investment in current reproduction. Under the “compensation hypothesis”, males living in low-quality habitats would increase their effort in order to improve nestlings’ survival and therefore their current reproductive success, while paying a large energetic cost possibly resulting in lower annual survival and reproduction during the following breeding season. Conversely, under the “prudent father hypothesis”, males in low-quality habitats would limit their effort in order not to compromise survival and future reproduction, but paying costs in terms of current reproductive success. (i.e. favouring brood reduction).

Materials and Methods

Study area and species

The study was performed between 2016 and 2020 in an area located in Western Switzerland, in a typical farmland landscape. Intensive crops cover the majority of the area, interspersed with villages and forests (Frey, Sonnay, Dreiss, & Roulin, 2010). Recently, agri-environment schemes (AES) were implemented in the landscape to maintain and promote biodiversity, including mainly extensively exploited meadows and pastures, wildflower strips and hedges. These areas host high densities and diversity of small mammals compared to surrounding intensively exploited crops, as shown by specific surveys which are periodically performed in the study area (Aschwanden 2007, Arlettaz 2011), and barn owls use them preferentially when hunting (Séchaud et al. 2021).

Nest boxes for barn owls have been installed in the study area since 1985 to counter the loss of natural breeding sites. Barn owl females produce an egg every 2-3 days and start incubating them as soon they are laid, resulting in a hatching asynchrony of several days between each nestling. Barn owls lay 6 eggs on average (from 1 to 11), from which 4 fledglings (from 0 to 9) are raised successfully (Frey et al. 2011). As some barn owls breed twice per season, with reproductive success varying between the first and second clutch (Frey et al. 2011, Béziers et al. 2016), we considered only first clutches in our analyses. Post-hatching parental investment varies between sexes, with males being the main prey providers (three quarters of the prey on average; Roulin 1999; 2002). In addition to being little involved in feeding the nestlings, females sometimes desert the nest to produce another clutch elsewhere (up to 59% of the females in certain years; Beziers et al. 2016), and this causes them to travel great distances in search of a free nesting site. Thus, at the time of our study, the home range of females might depend on many other factors than habitat quality, and we therefore did not consider them in our analyses.

GPS tag deployment

Breeding adults were captured at their nest site when the oldest nestling was 24.8 days old (SD=2.1; range: 19 to 30), using a well-established procedure (authorizations of the Department of the consumer and veterinary affairs: VD and FR 2844 and 3213; Séchaud et al. 2021). The age of the nestlings at the moment of GPS installation did not significantly varies with male's home range size (lmer: Estimates (SE)=-0-076 (0.177), *p*=0.668), thus indicating that nestling age could not have affected male home range size.

The males were equipped with small GPS devices fixed on their back with a Teflon harness. In 2016 and 2017, we used GiPSy-5 tags (Technosmart, Italy) programmed to collect the owl location every 10 seconds. In the three following years, we used Axy-Trek tags (Technosmart, Italy) with a 1-second interval sampling rate, which was re-sampled at 10 seconds in the present study to match the 2017 data. Both type of tags weighed approximately 12 grams including the battery and were packed in a protective plastic sheath for a final size of 30×20×10 mm, with an additional 40 mm long antenna. The barn owl being strictly nocturnal in Switzerland, we increased the GPS battery lifespan by turning the tags to standby mode during the day. The owls were recaptured on average 11 days later (range: 6 to 22 days), the tags recovered and the data stored in Movebank (www.movebank.org) under the project name "Barn owl (*Tyto alba*)" (ID 231741797). In total, we obtained 161 GPS tracks (32 in 2016; 18 in 2017; 40 in 2018; 39 in 2019; 32 in 2020), from 128 males (106 tracked once, 12 twice, 9 thrice and 1 fourth). Prior to any analysis, GPS data were filtered for aberrant positions using speed (excluding locations with a speed higher than 15 m/s) and location (excluding locations outside the study area). The final data set included 2'307'236 locations (out of the 2'309'883 collected in total).

Home range size and composition

For each individual, we estimated the 95% kernel home range using the *ctmm* R package (Calabrese, Fleming, & Gurarie, 2016) to account for the temporal auto-correlation present in our datasets (Fleming et al., 2015). To calibrate the *ctmm* model, we placed a GPS device on a pole in open landscape and used the data collected as User Equivalent Range Error (UERE). The model best fit was chosen automatically with the *variogram.fit* function in the same package. Variogram plots were then visually inspected and the home range size extracted. For the 22 males equipped two consecutive years, we estimated the Intraclass Correlation Coefficient (ICC) to measure the proportion of variance explained by the individual repeated measurement in different years. We found a moderate ICC of 0.54, meaning that an individual's home range size is not constant from one year to the next.

To investigate the quality of the habitat exploited by individual barn owl, we looked at the relation between home range size and the proportion of the main habitat features. We extracted the forest and settlement areas, two main components of the farmland landscape, from the Swiss Topographic Landscape Model catalogue. These two habitats have been shown to be avoided by barn owls when hunting (Séchaud et al., 2021), and were thus expected to be of poor quality. In contrast, AES were specifically implemented in farmland to promote biodiversity, and have been shown to be preferentially used by hunting barn owls (Séchaud et al., 2021), probably because they contain high densities of prey (Arlettaz et al., 2010; Aschwanden, Holzgang, & Jenni, 2007). AES surveys were obtained from the Department for Agriculture, Viticulture and Veterinary Affairs of the Vaud canton and the Department for Institutions, Agriculture and Forestry of the Fribourg canton. Among the 25 AES types present in the study area, we excluded the less abundant ones (representing <1km^2), as well as the AES types specific to a small region of the study area (and are thus available to only a few breeding pairs). The six remaining AES types were grouped in four main categories - extensive meadows, extensive pastures, wildflower strips and hedges – representing 93% of the AES surface implemented in the study area (Table S1). For the analyses, we used the total surface of AES present in the home range, as well as its Shannon Diversity Index estimated using the *vegan* package (Dixon, 2003).

Breeding and individual parameters

During the breeding season, the nest boxes were visited every month to find the ones occupied by breeding pairs. Once a clutch was found, we followed a standardized protocol of visits to the nest to record the following breeding parameters: number of eggs, nestlings and fledglings (Frey et al., 2010). The number of eggs was recorded a week before hatching, ensuring that all eggs were laid. The number of nestlings was recorded at the installation and recovery of the GPS (see *GPS tag deployment* above), as well as their wing length to estimate their growth during this period. To account for difference in timespan between installation and recovery of the GPS among males, we calculated a daily wing growth rate by dividing the increase in their length by the time elapsed between the measurements. Wing length was preferred to body mass as the latter can vary considerably with the recent consumption of a prey (e.g. the weight of a prey can reach up to 50% of the body mass of a nestling). We considered as “fledgling” all nestling that reached 55 days of age, which corresponds to their first flights out of the nest (Frey et al., 2010).

At the capture of the males for the GPS installation and recovery, we measured their body mass and wing length. As adults, their wing size does not change during the breeding season, so we estimated a daily body mass variation by dividing the difference in weight by the time between the two capture events. Even if this could be influenced by the consumption of a prey, adults are heavier than nestlings and thus the proportional effect of prey consumption is less impactful. In addition, body mass variation is a commonly used proxy of parental investment in bird studies (e.g. Bryant, 1988; Dijkstra et al., 1990; Merila & Wiggins, 1997). For each individual, we recorded its age based on ringing information (if it was previously ringed as nestling or as adult in the previous years) or feather moulting pattern (distinguishing yearlings from old birds; Taylor, 1994). Then, as not all birds could have been aged precisely, we classified them in two age groups, representing their previous breeding experience: yearlings (i.e. unexperienced) or old (i.e. experienced) individuals.

To measure the long-term effects of habitat quality on males, we recorded their annual survival and their breeding success the following year. We considered the males that did not breed the following year as not having survived the winter, a sensitive period for this species (Altwegg, Roulin, Kestenholz, & Jenni, 2006; Chausson, Henry, Almasi, & Roulin, 2014). It is also unlikely that they have left the study area as it is the young that disperse (van den Brink, Dreiss, & Roulin, 2012). The breeding success the following year was measured as the number of fledglings produced (see above for details).

Movement parameters

We measured the nightly distance covered by each bird as the sum of the distance between GPS locations per night recorded. We excluded the night of GPS installation (as the bird behaviour might have been altered by the capture) and the last night if not recorded completely. The nightly distance covered is not directly related to home range size, but rather to the number of feeding events and the time spent hunting on the wing. Thus, perching locations were excluded from the estimation of the nightly distance covered, as, when birds perch, the GPS locations differ slightly and could generate wrong distances (Séchaud et al., 2021). To this purpose, we used the Expectation-Maximization binary Clustering (EMbC) method implemented in the *EMbC* package to identify behaviour modes (Garriga, Palmer, Oltra, & Bartumeus, 2016). EMbC clusters movement data based on speed and turning angle between locations. Perching behavioural mode, due to small GPS location errors, was characterized by low speed and a wide range of turning angles, while movement behavioural mode was characterized by medium-high speed and medium-high turning angles (Séchaud et al., 2021). We compared EMbC classification with a visual classification of perching locations and found an average match of 94.5% (SE=2.3; San-Jose et al., 2019).

As one prey is brought per nest visit (Roulin et al., 1999), we estimated the nightly prey provisioning by counting the number of visits to the nest box per night. The visits were identified using the *recurse* package (Bracis, Bildstein, & Mueller, 2018) by setting a radius of 150 meters around the nest site and ignoring all excursions outside of the radius for less than 60 seconds. Using this procedure, we found an average prey provisioning of 8.8 prey delivered to the nest per night, which corresponds to the previous feeding rate reported for barn owls (Roulin, 2002b; Roulin et al., 1999). To further validate the method, we compared the visits obtained with the GPS tracks to visits assessed with camera traps installed in front of 10 nests. We found that 98.3% (range: 95.2 – 100%) of the visits corresponded to feeding events, and thus considered this method as highly reliable to assess prey provisioning.

Statistical analyses

Habitat quality

We modelled the effects of home range composition, as well as individual and temporal parameters on the home range size using a linear mixed-effect model in *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). The proportion of forest, settlements and AES in the home range, as well as the AES diversity, were included in the model as predictors of the home range size. Because the AES mapping started in 2018, no data were available for the two first years of our study (2016 and 2017). Hence, in this first model, we only considered the owls tagged from 2018 to 2020 (n=127). The bird's age category (yearling or old) and the laying date were also included as covariates, and the year of the observation was set as random factor. Considering that some individuals were captured and deployed with GPS in multiple years (see above) individual identity (hereafter individual ID) was also added to all the models. However, to check whether repeated measures of the same individuals would have affected the results, all the models were re-run using a single datum per individual (without individual ID as an additional random factor). These analyses always provided qualitatively similar results (details not shown for brevity), and therefore in the main text we reported the output of the models including the largest sample size. For this and all linear mixed-effect models, we first checked for collinearity between predictors and then verified the model assumptions by visually inspecting residual diagnostic plots.

Reproductive success

We investigated breeding success in relation to home range size at different development stages of the clutch (n=161), namely number of eggs (square root transformed) and fledglings, using linear mixed-effect models. The laying date, and the male's home range size and age (yearling or old) were included as covariates. The year of observation and the individual ID were included as random factors. The "fledgling" model also included the number of eggs laid as a covariate. Then, using the same covariates and random variables as for the "fledgling" model, we modelled the fledging success by comparing the number eggs that succeeded or failed to fledge using generalised linear mixed-effect models with a binomial distribution.

Finally, to study the daily nestling wing growth rate (between GPS installation and recovery, n=592), we built a model including laying date, the brood size, the nestling rank in the brood age hierarchy (rank number 1 is assigned to the oldest nestling), and the home range size and age of the father as covariates. We included an interaction between the home range size and the nestling rank as early- or late-hatched nestlings might be affected differently by the home range size. Year, individual ID and brood identity were included as random factors. As high ranks can be found only in big broods, we ran the same analysis considering only broods with a maximum of 5 nestlings.

Parental investment

To study potential mechanisms explaining the effect of habitat quality on fitness, we looked at father's prey provisioning rate, nightly distance covered and body mass variation (n=161). The "prey provisioning rate" was square root transformed, and the "nightly distance covered" log transformed, to meet the model assumptions. All three models included laying date, home range size, age and the number of nestlings as covariates, while the year of observation and individual ID were set as random factors. In addition, the "nightly distance covered" and the "daily body mass variation" models included also prey provisioning rate to account for the number of times that the bird went back and forth from the nest to deliver prey.

Annual survival and future reproduction

To study the effect of habitat quality on the males' long term breeding events, we investigated their annual survival and their future reproduction success (i.e. number of fledglings produced the following year). We modelled the "annual survival" using generalised linear mixed-effect models with a binomial distribution, and the "future reproduction" success using linear mixed-effect models. Both models included laying date, home range size, age and the number of nestlings as covariates, while the year of observation and individual ID were set as random factors.

Results

Home range size and habitat quality

The home range size of the male barn owls tracked ranged from 1.1 to 19.8 km^2 (mean=6.0 km^2; SD=3.7). We found that smaller home ranges contained higher proportion of AES than bigger ones. In contrast, bigger home ranges included a higher Shannon diversity of AES and a higher proportion of forested areas. Neither male age, nor laying date or the proportion of settlements affected the size of home ranges (Table 1).

Reproductive success

Although the number of eggs laid was not related to home range size, the number fledglings and the fledging success were higher for males with smaller home ranges (Table 2; Figure1). The number of eggs increased with laying date, but none of the other breeding parameters considered (fledglings and fledging success) were influenced by it. Male age had no effect in any of the models (Table 2).

When investigating nestling growth, we found a significant effect of the interaction between the nestling rank and the home range size (Table 3). Specifically, while growth rate of early-hatched nestlings was unaffected by home range size, late-hatched nestlings reared by males with large home range size suffered from a slower growth compared to those reared by males maintaining small or intermediate home range sizes (Figure 2). In addition, neither laying date, nor male age or the number of nestlings affected nestling growth (Table 3). The complementary analysis considering only broods with a maximum of 5 nestlings (to account that high ranks can only be found in big broods) presented similar results (Table S2).

Parental investment

Home range size predicted negatively prey provisioning rate and positively nightly distance covered (Figure 3; Table 4). Thus, males with smaller home ranges provided more prey to the nest, while covering fewer distances than males with larger ones. However, home range size did not affect male body mass variation. Brood size predicted positively prey provisioning rate (Figure 4a), but not the distance covered per night or the male body mass variation (Table 4). Laying date did not affect prey provisioning nor male body mass variation, but the distance covered significantly decreased with laying date although the effect was small. Prey provisioning rate predicted positively the distance covered nightly (Figure 4b), but not the body mass variation. Male age was not statistically significant in the different models.

Annual survival and future reproduction

Home range size did not predict the annual survival or the future reproduction success (Table 5). None of the other variables (male age, laying date, and brood size) included in the models showed a significant effect.

Discussion

In the present study we investigated how the quality of breeding environment, as gauged by home range size, predicts individual reproductive success and parental effort in a large number of barn owl males. We found that individuals breeding in high-quality habitats maintain smaller home ranges, because they include a large extent of the main habitats used by this species to hunt small mammals. Not surprisingly, these habitats are associated with a large presence of the main prey of the barn owl in the study area (Arlettaz et al., 2010; Aschwanden et al., 2007). This result is consistent with a large body literature on birds and mammals, spanning from primary consumers (Saïd et al., 2009; Van Beest et al., 2011) to top predators (Kittle et al., 2015), including other raptor species (Hakkarainen et al., 1997; Kouba et al., 2017; Mirski & Väli, 2021; Redpath, 1995; Rutz & Bijlsma, 2006; Santangeli et al., 2012). In practice, in high-quality habitats organisms are able to find more resources in the proximity of their breeding site, without the need to cover long distances to hunt, which may result in a smaller energetic and metabolic expenditure compared to those individuals that are forced to forage further (Altmann, 1987; Evens et al., 2018). This is particularly important during the rearing of altricial offspring, which need a large food supply to be sustained until fledging. Indeed, compatibly with this observation, we also found that males living in large home ranges have to cover a larger distance every night in order to provide food to their broods, which, however, are fed less frequently than those reared in high-quality habitats. Such a reduced feeding rate, which corresponds to a smaller food received because barn owl parents invariably provide a single prey item per feeding visit (Roulin et al., 1999), is the main candidate to explain why the fledging success of broods reared by males in large home ranges is smaller, although the number of eggs laid did not depend on male’s home range size. Again, this result finds ample correspondence in the literature, as several previous studies showed a negative relationship between home range size/habitat quality and feeding rate (Bruun & Smith, 2003; Hakkarainen et al., 1997; Redpath, 1995; Trembley et al., 2004), as well as reproductive success (Hakkarainen et al., 1997; Pfeiffer & Meyburg, 2015; Redpath, 1995), despite an increase of distance covered (Bruun & Smith, 2003; Hakkarainen et al., 1997; Trembley et al., 2004).

We also showed that the reduced fledging success is likely mediated by the death of the smallest nestlings of the broods raised by males with large home ranges. Indeed, although growth rate of early-hatched nestlings is similar among broods, that of late-hatched nestlings is considerably larger in broods reared in high-quality home ranges. Such an observation suggests that under condition of food shortage fathers may preferentially feed the offspring of higher reproductive value (e.g. Caro et al., 2016; Romano et al., 2016) and/or, more likely, larger and highly-competitive nestlings may monopolize the resources at the expense of their smaller siblings, as commonly observed in avian species (e.g. David M. Bryant & Tatner, 1990; Mock & Parker, 1986; Stenning, 1996), including the studied one (Roulin, Colliard, Russier, Fleury, & Grandjean, 2008). Therefore, males maintaining small, but environmentally-rich, home ranges are able to accomplish the rearing of a larger number of nestlings, without incurring in increased energetic costs. This is not the case for males hunting in large home ranges, which, because of the large distance covered, have to considerably enhance their hunting effort in order to provide an amount of food enough to successfully fledge all their offspring. However, we showed that these males did not pay such an increased cost, at least in terms of body mass variation during rearing. In practice, when breeding in low-quality habitats, barn owl males do not increase their parental investment in order to compensate for the lower prey abundance near the nest, and pay a cost in annual reproductive success (i.e. smaller number of fledglings) while saving their limiting energies for self-maintenance. We thus interpret this finding as an evidence consistent with the "prudent father hypothesis", with males trading-off their current fitness versus future breeding opportunities. This argument is also compatible with a previous study of the same population, where an experimental increase in brood size resulted in smaller nestling growth and pre-fledging survival, but in a lack of any long-term effect on parental fitness (Roulin et al., 1999). Hence, when broods require an extra parental effort, for example due to a suboptimal environmental conditions (this study) or an increased number of nestlings to be fed (Roulin et al., 1999), parents do not jeopardize their future reproduction, and favour brood reduction. An additional piece of evidence in line with the above reasoning is that males breeding in large home ranges do not pay any long-term cost in terms of survival or future breeding opportunities, as they have the same likelihood of reproducing as well as a similar reproductive success than the other males in the breeding season following the one for which we measured breeding habitat quality.

We have to note that the correlative nature of the present study prevents us from inferring causality and that some of the obtained results could be partly affected by confounding factors. Indeed, without an experimental manipulation linking food abundance and home range size (see e.g. Santangeli et al., 2012), we can only hypothesize that variation in home range size, annual fitness and reproductive investment are due to prey availability in different habitats. In addition, considering that male previous breeding experience (i.e. age) does not predict any of the variables under investigation (including fledging success and the probability of reproducing in the following breeding season), we cannot rule out the possibility that intrinsic individual quality might affect both hunting ability and annual fitness, with high-quality individuals being more efficient in capturing prey in the proximity of their nest and feed their brood more frequently, or simply being more able to breed in a good-quality habitat. However, preliminary analyses failed to find some associations between male phenotypic traits previously associated with quality and home range size (e.g. wing length and plumage colour; details not shown), thus making this possibility an unlikely one. However, even if our results would have been affected by individual quality, we note that the relationships between habitat quality, parental effort and reproductive success are still maintained. Finally, although female contribution to nestling feeding is much lower than that of males (Roulin et al., 1999), with the present data we could not account for maternal effort in hunting, and therefore in fledging success.

On the one hand, females might have contributed more to parental care in low-quality habitats in order to compensate the lower male feeding rate (e.g. Harrison, Barta, Cuthill, & Székely, 2009; Osorno & Székely, 2004; Paredes, Jones, & Boness, 2006). Under such circumstance, female behaviour would have therefore masked the observable effects of habitat quality, thus making our results very conservative. On the other hand, females might have contributed more to feeding nestlings in good-quality habitats, because of a lower cost of providing food to their broods. In such case, a larger female investment would have exacerbated the effects. However, we note that if this is the case, an eventual increase of maternal effort would have been a consequence of habitat quality in the surrounding of the nest.

A final consideration that it is worthy to mention here is that, irrespectively of the mechanisms determining reproductive success, from a conservation point of view, our results show that AES, adopted to limit the strong increase in farmland biodiversity, seems to be beneficial for the barn owl. This is an additional, though collateral, novel finding of our study. Indeed, despite documented positive effects on plant, insect and small mammal density and species richness (e.g. Kleijn et al., 2006; Zingg, Ritschard, Arlettaz, & Humbert, 2019), the effects of AES for larger vertebrates remained uncertain. The present results therefore enforce the conviction that proper conservation policies involving citizenship (i.e. farmers) can have a positive effect on the entire natural communities.

In conclusion, in this study performed on a large sample of individuals, we showed that habitat quality affects annual reproductive success and individual trade-offs in the barn owl. Indeed, males exposed to limiting ecological conditions did not increase their parental investment to compensate for the lower prey abundance near the nest, and, by favouring brood reduction, traded-off their current fitness against future breeding opportunities.

Acknowledgements

We thank A.P. Machado; L. Ançay, C. Gémard, S. Zurkinden, N. Külling, A-C. Heinz, E. Mayor, C. Plancherel, R. Sartori, G. Perroud, P. Ducouret, C. Massa, C. Sahli, M. Déturche, M. Chèvre, J. Ehinger, N. Apolloni and R.Bühler for their help in collecting field data. This study was financially supported by the Swiss National Science Foundation (grants no. 31003A_173178).

References

Altmann, S. A. (1987). The impact of locomotor energetics on mammalian foraging. *Journal of Zoology*, *211*(2), 215–225. doi:10.1111/j.1469-7998.1987.tb01530.x

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

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. *Journal of Ornithology*, *151*(3), 553–564. doi:10.1007/s10336-009-0485-0

Aschwanden, J., Holzgang, O., & Jenni, L. (2007). Importance of ecological compensation areas for small mammals in intensively farmed areas. *Wildlife Biology*, *13*(2), 150–158. doi:10.2981/0909-6396(2007)13[150:IOECAF]2.0.CO;2

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi:10.18637/jss.v067.i01

Béziers, P., & Roulin, A. (2016). Double brooding and offspring desertion in the barn owl *Tyto alba*. *Journal of Avian Biology*, *47*(2), 235–244. doi:10.1111/jav.00800

Bókony, V., Lendvai, Á. Z., Likér, A., Angelier, F., Wingfield, J. C., & Chastel, O. (2009). Stress Response and the value of reproduction: Are birds prudent parents? *American Naturalist*, *173*(5), 589–598. doi:10.1086/597610

Bracis, C., Bildstein, K. L., & Mueller, T. (2018). Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography*, *41*(11), 1801–1811. doi:10.1111/ecog.03618

Bruun, M., & Smith, H. G. (2003). Landscape composition affects habitat use and foraging flight distances in breeding European starlings. *Biological Conservation*, *114*(2), 179–187. doi:10.1016/S0006-3207(03)00021-1

Bryant, D. M. (1988). Energy expenditure and body mass changes as measures of reproductive costs in birds. *Functional Ecology*, *2*(1), 23. doi:10.2307/2389456

Bryant, David M., & Tatner, P. (1990). Hatching asynchrony, sibling competition and siblicide in nestling birds: Studies of swiftlets and bee-eaters. *Animal Behaviour*, *39*(4), 657–671. doi:10.1016/S0003-3472(05)80377-X

Budden, A. E., & Beissinger, S. R. (2009). Resource allocation varies with parental sex and brood size in the asynchronously hatching green-rumped parrotlet (*Forpus passerinus*). *Behavioral Ecology and Sociobiology*, *63*(5), 637–647. doi:10.1007/s00265-008-0698-x

Calabrese, J. M., Fleming, C. H., & Gurarie, E. (2016). ctmm : an R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution*, *7*(9), 1124–1132. doi:10.1111/2041-210X.12559

Candolin, U. (1998). Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1402), 1171–1175. doi:10.1098/rspb.1998.0415

Caro, S. M., Griffin, A. S., Hinde, C. A., & West, S. A. (2016). Unpredictable environments lead to the evolution of parental neglect in birds. *Nature Communications*, *7*(1), 1–10. doi:10.1038/ncomms10985

Castañeda, X. A., Huysman, A. E., & Johnson, M. D. (2021). Barn Owls select uncultivated habitats for hunting in a winegrape growing region of California. *Ornithological Applications*, *123*(1), 1–15. doi:10.1093/ornithapp/duaa058

Charnov, E. L., & Krebs, J. R. (1974). On clutch-size and fitness. *Ibis*, *116*(2), 217–219. doi:10.1111/j.1474-919X.1974.tb00241.x

Chausson, A., Henry, I., Almasi, B., & Roulin, A. (2014). Barn Owl (Tyto alba) breeding biology in relation to breeding season climate. *Journal of Ornithology*, *155*(1), 273–281.

Cox, R. M., Parker, E. U., Cheney, D. M., Liebl, A. L., Martin, L. B., & Calsbeek, R. (2010). Experimental evidence for physiological costs underlying the trade-off between reproduction and survival. *Functional Ecology*, *24*(6), 1262–1269. doi:10.1111/j.1365-2435.2010.01756.x

Daan, S., Deerenberg, C., & Dijkstra, C. (1996). Increased Daily Work Precipitates Natural Death in the Kestrel. *The Journal of Animal Ecology*, *65*(5), 539. doi:10.2307/5734

Dijkstra, C., Daan, S., & Tinbergen, J. M. (1990). Family Planning in the Kestrel (*Falco Tinnunculus*): The Ultimate Control of Covariation of Laying Date and Clutch Size. *Behaviour*, *114*(1–4), 83–116. doi:10.1163/156853990X00068

Dixon, P. (2003, December 1). VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science*. Opulus Press AB. doi:10.1111/j.1654-1103.2003.tb02228.x

Drent, R. H., & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Adrea*, *68*, 225–263. doi:10.5253/arde.v68.p225

Evens, R., Beenaerts, N., Neyens, T., Witters, N., Smeets, K., & Artois, T. (2018). Proximity of breeding and foraging areas affects foraging effort of a crepuscular, insectivorous bird. *Scientific Reports*, *8*(1), 1–11. doi:10.1038/s41598-018-21321-0

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2015). Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology*, *96*(5), 1182–1188. doi:10.1890/14-2010.1

Frey-Roos, F., Brodmann, P. A., & Reyer, H. U. (1995). Relationships between food resources, foraging patterns, and reproductive success in the water pipit, *Anthus sp. Spinoletta*. *Behavioral Ecology*, *6*(3), 287–295. doi:10.1093/beheco/6.3.287

Frey, C., Sonnay, C., Dreiss, A., & Roulin, A. (2010). Habitat, breeding performance, diet and individual age in Swiss Barn Owls (*Tyto alba*). *Journal of Ornithology*, *152*(2), 279–290. doi:10.1007/s10336-010-0579-8

Garriga, J., Palmer, J. R. B., Oltra, A., & Bartumeus, F. (2016). Expectation-Maximization Binary Clustering for Behavioural Annotation. *PLOS ONE*, *11*(3), e0151984. doi:10.1371/journal.pone.0151984

Ghalambor, C. K., & Martin, T. E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, *292*(5516), 494–497. doi:10.1126/science.1059379

Hakkarainen, H., Koivunen, V., & Korpimäki, E. (1997). Reproductive success and parental effort of Tengmalm's owls: Effects of spatial and temporal variation in habitat quality. *Ecoscience*, *4*(1), 35–42. doi:10.1080/11956860.1997.11682374

Harrison, F., Barta, Z., Cuthill, I., & Székely, T. (2009). How is sexual conflict over parental care resolved? A meta-analysis. *Journal of Evolutionary Biology*, *22*(9), 1800–1812. doi:10.1111/j.1420-9101.2009.01792.x

Harshman, L. G., & Zera, A. J. (2007). The cost of reproduction: the devil in the details. *Trends in Ecology and Evolution*, *22*(2), 80–86. doi:10.1016/j.tree.2006.10.008

Hinam, H. L., & Clair, C. C. S. (2008). High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of Northern saw-whet owls. *Biological Conservation*, *141*(2), 524–535. doi:10.1016/j.biocon.2007.11.011

Hindmarch, S., Elliott, J. E., Mccann, S., & Levesque, P. (2017). Habitat use by barn owls across a rural to urban gradient and an assessment of stressors including, habitat loss, rodenticide exposure and road mortality. *Landscape and Urban Planning*, *164*, 132–143.

doi:10.1016/j.landurbplan.2017.04.003

Hinsley, S. A., Rothery, P., & Bellamy, P. E. (1999). Influence of Woodland Area on Breeding Success in Great Tits Parus major and Blue Tits *Parus caeruleus*. *Journal of Avian Biology*, *30*(3), 271. doi:10.2307/3677353

Kaiser, S. A., Scott Sillett, T., Risk, B. B., & Webster, M. S. (2015). Experimental food supplementation reveals habitat-dependent male reproductive investment in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1803). doi:10.1098/rspb.2014.2523

Kittle, A. M., Anderson, M., Avgar, T., Baker, J. A., Brown, G. S., Hagens, J., … Fryxell, J. M. (2015). Wolves adapt territory size, not pack size to local habitat quality. *Journal of Animal Ecology*, *84*(5), 1177–1186. doi:10.1111/1365-2656.12366

Kleijn, D., Baquero, R. A., Clough, Y., Díaz, M., Esteban, J., Fernández, F., … Yela, J. L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, *9*(3), 243–254. doi:10.1111/j.1461-0248.2005.00869.x

Kouba, M., Bartoš, L., Sindelář, J., & St’astny, K. (2017). Alloparental care and adoption in Tengmalm’s Owl (Aegolius funereus). *Journal of Ornithology*, *158*, 185–191. doi:10.1007/s10336-016-1381-z

Laaksonen, T., Hakkarainen, H., & Korpimäki, E. (2004). Lifetime reproduction of a forest-dwelling owl increases with age and area of forests. *Proceedings of the Royal Society B: Biological Sciences*, *271*(SUPPL. 6). doi:10.1098/rsbl.2004.0221

Lack, D. (1947). The Significance of Clutch-size. *Ibis*, *89*(2), 302–352. doi:10.1111/j.1474-919X.1947.tb04155.x

Marshall, K. E., & Sinclair, B. J. (2010). Repeated stress exposure results in a survival-reproduction trade-off in *Drosophila melanogaster*. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1683), 963–969. doi:10.1098/rspb.2009.1807

Martin, T. E. (1987). Food as a limit on breeding birds : a life-history perspective. *Annual Review of Ecology and Systematics*, *18*, 435–487.

McGinley, M. A., Temme, D. H., & Geber, M. A. (1987). Parental investment in offspring in variable environments: theoretical and empirical considerations. *American Naturalist*, *130*(3), 370–398. doi:10.1086/284716

Merilä, J., & Fry, J. D. (1998). Genetic Variation and Causes of Genotype-Environment Interaction in the Body Size of Blue Tit (*Parus caeruleus*). *Genetics*, *148*(3), 1233–1244.

Merilä, J., & Wiggins, D. A. (1997). Mass Loss in Breeding Blue Tits: The Role of Energetic Stress. *The Journal of Animal Ecology*, *66*(4), 452. doi:10.2307/5940

Mirski, P., & Väli, Ü. (2021). Movements of birds of prey reveal the importance of tree lines, small woods and forest edges in agricultural landscapes. *Landscape Ecology*, 1–13. doi:10.1007/s10980-021-01223-9

Mock, D. W., & Parker, G. A. (1986). Advantages and disadvantages of egret and heron brood reduction. *Evolution*, *40*(3), 459–470. doi:10.1111/j.1558-5646.1986.tb00499.x

Nilsson, J. A., & Svenssonn, E. (1996). The cost of reproduction: A new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, *263*(1371), 711–714. doi:10.1098/rspb.1996.0106

Osorno, J. L., & Székely, T. (2004). Sexual conflict and parental care in magnificent frigatebirds: Full compensation by deserted females. *Animal Behaviour*, *68*(2), 337–342. doi:10.1016/j.anbehav.2003.06.027

Paredes, R., Jones, I. L., & Boness, D. J. (2006). Parental roles of male and female thick-billed murres and razorbills at the Gannet Islands, Labrador. *Behaviour*, *143*(4), 451–481. doi:10.1163/156853906776240641

Perrins, C. M. (1965). Population Fluctuations and Clutch-Size in the Great Tit, *Parus major*. *The Journal of Animal Ecology*, *34*(3), 601. doi:10.2307/2453

Pfeiffer, T., & Meyburg, B. U. (2015). GPS tracking of Red Kites (*Milvus milvus*) reveals fledgling number is negatively correlated with home range size. *Journal of Ornithology*, *156*(4), 963–975. doi:10.1007/s10336-015-1230-5

Redpath, S. M. (1995). Habitat Fragmentation and the Individual: Tawny Owls *Strix aluco* in Woodland Patches. *The Journal of Animal Ecology*, *64*(5), 652. doi:10.2307/5807

Reznick, D. (1985). Costs of Reproduction: An Evaluation of the Empirical Evidence. *Oikos*, *44*(2), 257. doi:10.2307/3544698

Ricklefs, R. E. (1977). On the Evolution of Reproductive Strategies in Birds: Reproductive Effort. *The American Naturalist*, *111*(979), 453–478. doi:10.1086/283179

Rivalan, P., Prévot-Julliard, A. C., 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*(4), 564–574. doi:10.1007/s00442-005-0159-4

Roff, D. A., Mostowy, S., & Fairbairn, D. J. (2002). The evolution of trade-offs: Testing predictions on response to selection and environmental variation. *Evolution*, *56*(1), 84–95. doi:10.1111/j.0014-3820.2002.tb00851.x

Romano, A., Costanzo, A., Caprioli, M., Parolini, M., Ambrosini, R., Rubolini, D., & Saino, N. (2016). Better-surviving barn swallow mothers produce more and better-surviving sons. *Evolution*, *70*(5), 1120–1128. doi:10.1111/evo.12908

Romano, A., Séchaud, R., & Roulin, A. (2020). Global biogeographical patterns in the diet of a cosmopolitan avian predator. *Journal of Biogeography*, *47*(7), 1467–1481. doi:10.1111/jbi.13829

Roulin, A. (1999). Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. *Behavioral Ecology*, *10*(6), 688–695. doi:10.1093/beheco/10.6.688

Roulin, A. (2002a). Offspring Desertion by Double-Brooded Female Barn Owls (*Tyto alba*). *The Auk*, *119*(2), 515–519. doi:10.2307/4089898

Roulin, A. (2002b). Tyto alba Barn Owl. *BWP Update*, *4*(2), 115–138.

Roulin, A. (2004). Covariation between plumage colour polymorphism and diet in the Barn Owl *Tyto alba*. *Ibis*, *146*(3), 509–517.

Roulin, A., Colliard, C., Russier, F., Fleury, M., & Grandjean, V. (2008). Sib-sib communication and the risk of prey theft in the barn owl *Tyto alba*. *Journal of Avian Biology*, *39*(6), 593–598. doi:10.1111/j.1600-048X.2008.04472.x

Roulin, A., Ducrest, A.-L., & Dijkstra, C. (1999). Effect of brood size manipulations on parents and offspring in the barn owl *Tyto alba*. *Ardea*, *87*(1), 91–100.

Rutz, C., & Bijlsma, R. G. (2006). Food-limitation in a generalist predator. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1597), 2069–2076. doi:10.1098/rspb.2006.3507

Saïd, S., Gaillard, J. M., Widmer, O., Débias, F., Bourgoin, G., Delorme, D., & Roux, C. (2009). What shapes intra-specific variation in home range size? A case study of female roe deer. *Oikos*, *118*(9), 1299–1306. doi:10.1111/j.1600-0706.2009.17346.x

San-Jose, L. M., Séchaud, R., Schalcher, K., Judes, C., Questiaux, A., Oliveira-Xavier, A., … Roulin, A. (2019). Differential fitness effects of moonlight on plumage colour morphs in barn owls. *Nature Ecology and Evolution*, *3*(9), 1331–1340. doi:10.1038/s41559-019-0967-2

Santangeli, A., Hakkarainen, H., Laaksonen, T., & Korpimäki, E. (2012). Home range size is determined by habitat composition but feeding rate by food availability in male Tengmalm's owls. *Animal Behaviour*, *83*(4), 1115–1123. doi:10.1016/j.anbehav.2012.02.002

Séchaud, R., Schalcher, K., Machado, A. P., Almasi, B., Massa, C., Safi, K., & Roulin, A. (2021). Behaviour-specific habitat selection patterns of breeding barn owls. *Movement Ecology*, *9*(1), 18. doi:10.1186/s40462-021-00258-6

Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, O., & Husby, M. (1984). On the adaptive value of intraclutch egg-size variation in birds. *Auk*, *101*(4), 685–697. doi:10.2307/4086895

Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University.

Stenning, M. J. (1996). Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. *Trends in Ecology and Evolution*, *11*(6), 243–246. doi:10.1016/0169-5347(96)10030-6

Taylor, I. (1994). *Barn Owls: Predator-Prey Relationships and Conservation*. Cambridge University Press.

Trembley, I., Thomas, D., Blondel, J., Perret, P., & Lambrechts, M. M. (2004). The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. *Ibis*, *147*(1), 17–24. doi:10.1111/j.1474-919x.2004.00312.x

Tripet, F., Richner, H., & Tripet, F. (1997). Host responses to ectoparasites: food compensation by parent blue tits. *Oikos*, *78*(3), 557. doi:10.2307/3545617

Turcotte, Y., & Desrochers, A. (2003). Landscape-dependent response to predation risk by forest birds. *Oikos*, *100*(3), 614–618. doi:10.1034/j.1600-0706.2003.12234.x

Van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M., & Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology*, *80*(4), 771–785. doi:10.1111/j.1365-2656.2011.01829.x

van den Brink, V., Dreiss, A. N., & Roulin, A. (2012). Melanin-based coloration predicts natal dispersal in the barn owl, *Tyto alba* . *Animal Behaviour*, *84*(4), 805–812. doi:10.1016/j.anbehav.2012.07.001

Walker, R. S., Gurven, M., Burger, O., & Hamilton, M. J. (2008). The trade-off between number and size of offspring in humans and other primates. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1636), 827–833. doi:10.1098/rspb.2007.1511

Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's

Principle. *The American Naturalist*, *100*(916), 687–690. doi:10.1086/282461

Zingg, S., Ritschard, E., Arlettaz, R., & Humbert, J. Y. (2019). Increasing the proportion and quality of land under agri-environment schemes promotes birds and butterflies at the landscape scale. *Biological Conservation*, *231*, 39–48. doi:10.1016/j.biocon.2018.12.022

Tables

Table 1: Male home range size in relation to male age, laying date and home range composition. Results of a linear mixed-effect model with the year of observation and the individual identity set as random factors, including 127 home ranges measured between 2018 and 2020. Home range size was log-transformed. Standardized estimates are provided. AES stands for agri-environment schemes, habitat types implemented in the study area to promote biodiversity.

Predictors	*Estimates (SE)*	*t*	*p*
(Intercept)	1.665 (0.106)	15.771	**<0.001**
Age (old)	-0.007 (0.111)	-0.064	0.949
Laying Date	-0.043 (0.056)	-0.766	0.446
Settlement proportion	0.028 (0.054)	0.517	0.606
Forest proportion	0.158 (0.052)	3.022	**0.003**
AES proportion	-0.155 (0.062)	-2.553	**0.012**
AES diversity	0.167 (0.060)	2.765	**0.007**

Table 2: Number of eggs, number of fledglings and fledging success in relation to male home range size. Results of two linear (number of eggs and number of fledglings) and one generalised linear (fledging success) mixed-effect models with the year of observation and the individual identity set as random factors, including 161 home ranges measured between 2016 and 2020. The number of eggs was square root transformed, and the fledging success model compared the number of eggs laid to the number of fledglings produced. Standardized estimates are provided.

	Number of eggs			**Number of fledglings**			**Fledging success**		
Predictors	*Estimates (SE)*	*t*	*p*	*Estimates (SE)*	*t*	*p*	*Estimates (SE)*	*t*	*p*
(Intercept)	2.518 (0.052)	48.147	**<0.001**	3.839 (0.145)	26.428	**<0.001**	0.579 (0.109)	5.288	**<0.001**
Age (old)	-0.023 (0.048)	-0.488	0.627	0.155 (0.204)	0.758	0.450	0.116 (0.147)	0.790	0.430
Laying date	0.078 (0.023)	3.341	**0.001**	-0.014 (0.103)	-0.131	0.896	-0.006 (0.072)	-0.079	0.937
Home range size	-0.026 (0.023)	-1.172	0.243	-0.214 (0.097)	-2.201	**0.029**	-0.166 (0.073)	-2.281	**0.023**
Number of eggs				0.261 (0.101)	2.582	**0.011**	-0.424 (0.074)	-5.719	**<0.001**

Table 3: Nestling growth rate in relation to its position in the brood age-hierarchy (rank) and male home range size. Results of a linear mixed-effect model including 740 nestlings, with the year of observation and the brood identity set as random factors. Standardized estimates are provided.

Predictors	*Estimates (SE)*	*t*	*p*
(Intercept)	5.491 (0.058)	94.777	**<0.001**
Age (old)	-0.036 (0.081)	-0.446	0.657
Date	0.019 (0.040)	0.481	0.631
Home range size	-0.059 (0.039)	-1.525	0.129
Number of nestlings	-0.041 (0.041)	-0.998	0.320
Rank	-0.089 (0.034)	-2.574	**0.010**
Home range size * Rank	-0.100 (0.039)	-2.573	**0.009**

Table 4: Male prey provisioning rate, nightly distance covered and daily body mass variation in relation to its home range size. Results of linear mixed-effect models with the year of observation and the individual identity set as random factors, including 161 home ranges measured between 2016 and 2020. The prey provisioning rate was square root transformed, and the distance covered was log-transformed. Standardized estimates are provided.

	Prey provisioning			**Distance covered**			**Body mass variation**		
Predictors	*Estimates (SE)*	*t*	*p*	*Estimates (SE)*	*t*	*p*	*Estimates (SE)*	*t*	*p*
(Intercept)	2.922 (0.160)	18.269	**<0.001**	3.285 (0.098)	33.651	**<0.001**	0.191 (0.223)	0.859	0.407
Age (old)	-0.049 (0.074)	-0.660	0.510	-0.074 (0.045)	-1.637	0.104	-0.058 (0.316)	-0.185	0.854
Laying date	0.031 (0.036)	0.840	0.402	-0.053 (0.022)	-2.341	**0.021**	0.196 (0.158)	1.242	0.217
Home range size	-0.119 (0.035)	-3.366	**0.001**	0.158 (0.022)	7.050	**<0.001**	-0.032 (0.155)	-0.204	0.838
Brood size	0.113 (0.036)	3.184	**0.002**	-0.013 (0.023)	-0.566	0.572	0.245 (0.156)	1.576	0.117
Prey provisioning rate				0.233 (0.026)	9.023	**<0.001**	-0.319 (0.167)	-1.909	0.065

Table 5: Male annual survival and future reproduction (number of fledglings produced the next year) in relation to its home range size. Results of a generalised linear mixed-effect models with a binomial distribution (annual survival model) and a linear mixed-effect model (future reproduction model) with the year of observation and the individual identity set as random factors, including respectively 129 and 56 home ranges measured between 2016 and 2019. Standardized estimates are provided.

	Annual survival			**Future reproduction**		
Predictors	*Estimates (SE)*	*t*	*p*	*Estimates (SE)*	*t*	*p*
(Intercept)	-1.433 (1.191)	-1.203	0.229	5.250 (0.423)	12.422	**<0.001**
Age (old)	0.624 (0.576)	1.083	0.279	0.144 (0.507)	0.285	0.776
Laying date	-0.009 (0.296)	-0.030	0.976	0.328 (0.245)	1.336	0.181
Home range size	0.412 (0.281)	1.464	0.143	-0.023 (0.241)	-0.094	0.925
Brood size	-0.026 (0.276)	-0.094	0.925	-0.159 (0.233)	-0.683	0.495

Figures

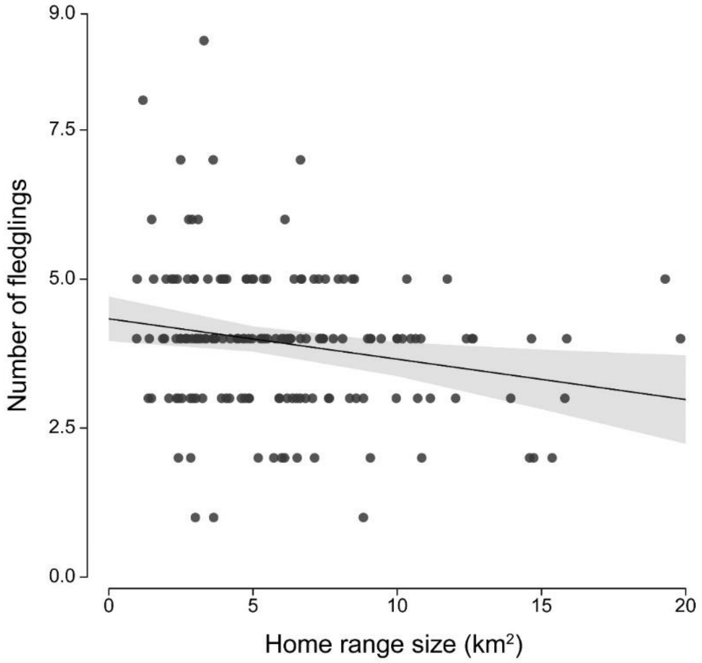


Figure 1: Number of fledglings produced in relation to male home range size (n=161). The continuous line represents the predicted number of nestlings in relation to male home range size, and the grey area the 95% confidence intervals associated (from the model reported in Table 2).

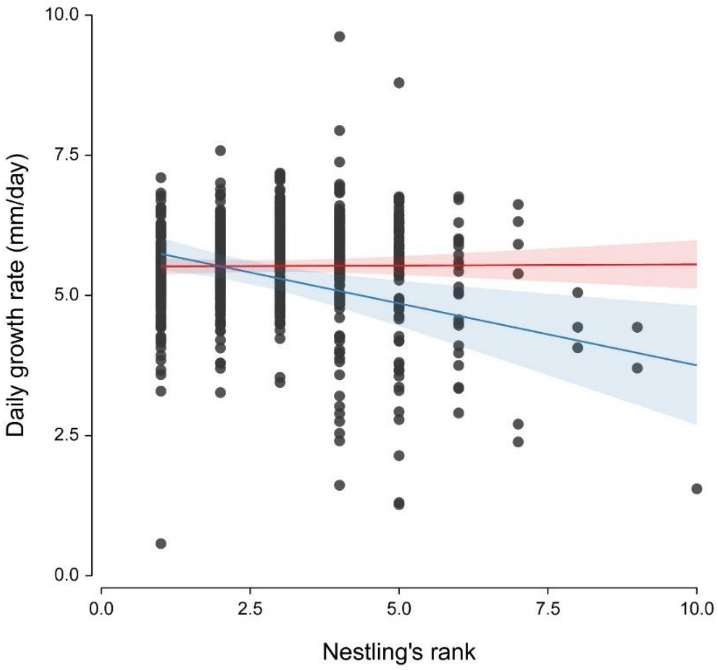


Figure 2: Nestling daily growth rate (n=592) in relation to its rank and male home range size. The continuous lines represent the predicted nestling's growth rate in relation to its rank, and the shaded areas the 95% confidence intervals associated (from the model reported in Table 3). The blue and red lines represent, respectively, the smallest (1.0 km^2) and the biggest (19.8 km^2) home ranges. This division was arbitrarily chosen to facilitate the visualisation of the result.

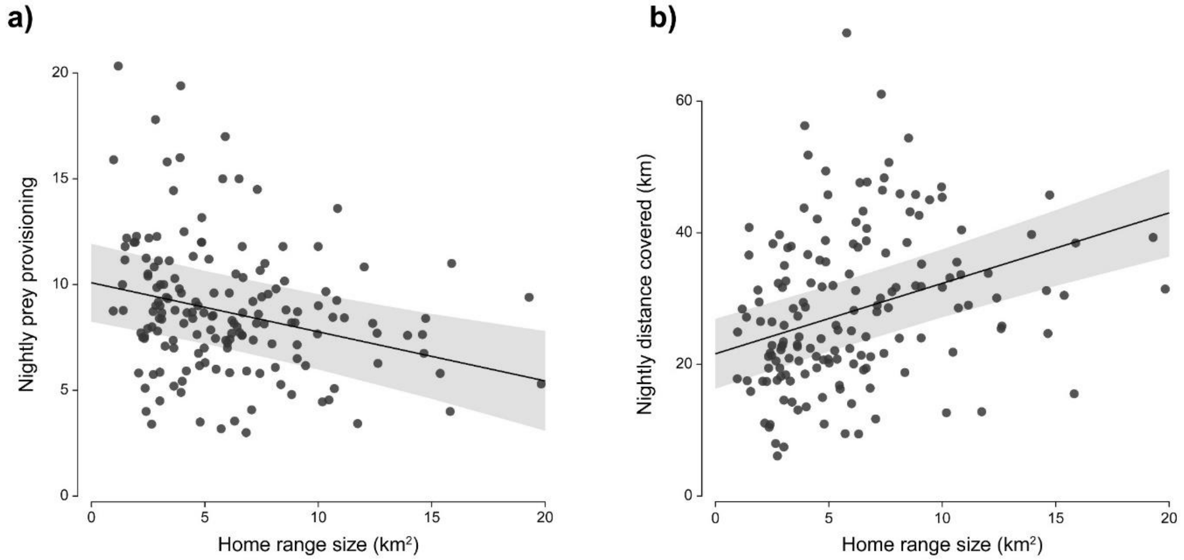


Figure 3: Male prey provisioning rate and nightly distance covered in relation to their home range size. The continuous lines represent a) the predicted prey provisioning rate and b) the predicted distance covered per night in relation to male home range size, and the grey area the 95% confidence intervals associated (from the models reported in Table 4)

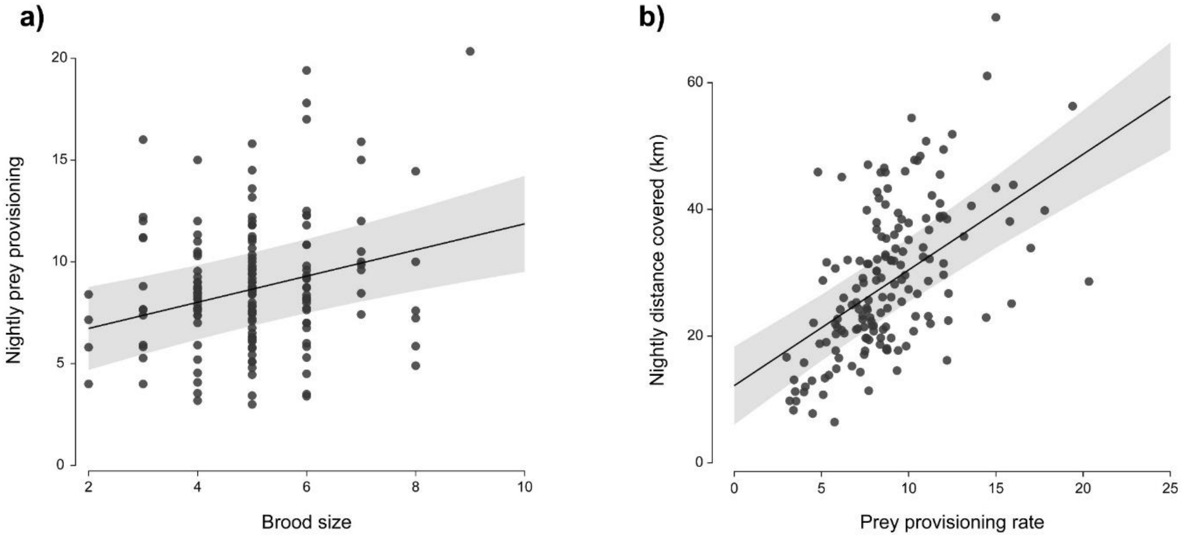


Figure 4: Effects of a) brood size on males provisioning rate, and of b) males' provisioning rate on the distance they cover per night. The continuous lines represent the predicted values, and the grey area the 95% confidence intervals associated (from the models reported in Table 4).

Chapter 2 – Supplementary information

Table S1: List of the 26 AES types present in the study area, with their respective surface in Km^2 during the three years of survey. The most abundant ones (>1km^2) were grouped in four categories - extensive meadows, extensive pastures, wildflower strips and hedges. The AES types 921 (high-stem orchard) and 717 (extensive vineyards) were excluded from the analyses as they are not present in the entire study area.

AES identifier	AES category	Surface in 2018	Surface in 2019	Surface in 2020
611	extensive meadows	71.756	71.481	72.367
617	extensive pastures	23.178	23.456	23.550
612	extensive meadows	8.252	8.365	8.348
852	hedges	5.138	5.209	5.288
556	wildflower strips	5.041	5.106	5.230
921	-	3.949	4.008	3.995
717	-	2.404	2.415	2.631
557	wildflower strips	0.999	1.009	1.029
924	-	0.620	0.634	0.630
851	-	0.504	0.479	0.461
559	-	0.382	0.378	0.348
634	-	0.122	0.126	0.149
904	-	0.083	0.095	0.143
694	-	0.075	0.056	0.134
618	-	0.014	0.029	0.119
922	-	0.131	0.115	0.116
572	-	0.112	0.127	0.112
55502	-	0.075	0.095	0.083
594	-	0.012	0.057	0.040
905	-	0.008	0.006	0.013
55501	-	0.002	0.000	0.004
693	-	0.002	0.002	0.002
908	-	0.003	0.003	0.002
923	-	0.000	0.001	0.002
906	-	0.001	0.001	0.001
55503	-	0.018	0.011	0.000
Total		122.881	123.263	124.796

Table S2: Nestling growth rate in relation to its position in the brood age-hierarchy (rank) and male home range size. Only broods containing 5 or less nestlings were considered (see Table 3 for the full analysis). Results of a linear mixed-effect model including 592 nestlings, with the year of observation and the brood identity set as random factors. Standardized estimates are provided.

Predictors	*Estimates (SE)*	*t*	*p*
(Intercept)	5.531 (0.069)	80.354	<0.001
Age (old)	-0.082 (0.096)	-0.848	0.399
Laying date	0.046 (0.047)	0.961	0.338
Home range size	-0.038 (0.044)	-0.871	0.385
Number of nestlings	-0.049 (0.043)	-1.124	0.263
Rank	-0.037 (0.035)	-1.042	0.298
Home range size * Rank	-0.118 (0.038)	-3.105	**0.002**

Chapter 3

Differential fitness effects of moonlight on plumage colour morphs in barn owls

Luis M. San-Jose[1], Robin Séchaud[1], kim Schalcher[1], Clarisse Judes[1], Anastasia Questiaux[1], Aymeric Oliveira-Xavier[1], Charlène Gémard[1], Bettina Almasi[2], Paul Béziers[1], Almut Kelber[3], Arjun Amar[4] and Alexandre Roulin[1]

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

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

[3] Lund Vision Group, Department of Biology, Lund University, Lund, Sweden.

[4] FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa

Chapter Status:

Published in Nature Ecology & Evolution

https://doi.org/10.1038/s41559-019-0967-2

Author contributions:

A.R., A.A. and L.M.S.-J. conceived and designed the study. A.R., P.B., B.A., R.S., K.S. and C.G. collected the field data on barn owls. R.S., K.S. and C.G. conducted the GPS-tracking study with contributions from P.B. and B.A. L.M.S.-J., C.J., A.Q. and A.O.-X. designed and conducted the behavioural experiments with voles. L.M.S.-J. conducted the statistical analysis with the contribution of R.S. L.M.S.-J. and A.R. wrote the paper, with major contributions from A.R., A.K., and R.S. and with input from all co-authors.

nature ecology & evolution

ARTICLES

https://doi.org/10.1038/s41559-019-0967-2

Differential fitness effects of moonlight on plumage colour morphs in barn owls

Luis M. San-Jose[1]*, Robin Séchaud[1], Kim Schalcher[1], Clarisse Judes[1], Anastasia Questiaux[1], Aymeric Oliveira-Xavier[1], Charlène Gémard[1], Bettina Almasi[2], Paul Béziers[1], Almut Kelber[3], Arjun Amar[4] and Alexandre Roulin[1]*

The Moon cycle exposes nocturnal life to variation in environmental light. However, whether moonlight shapes the fitness of nocturnal species with distinct colour variants remains unknown. Combining data from long-term monitoring, high-resolution global positioning system tracking and experiments using prey, we show that barn owls (*Tyto alba*) with distinct plumage colourations are differently affected by moonlight. The reddest owls are less successful at hunting and providing food to their offspring during moonlit nights, which associates with lower body mass and lower survival of the youngest nestlings and with female mates starting to lay eggs at low moonlight levels. Although moonlight should make white owls more conspicuous to prey, it either positively affects or does not affect the hunting and fitness of the whitest owls. We experimentally show that, under full-moon conditions, white plumage triggers longer freezing times in prey, which should facilitate prey catchability. We propose that the barn owl's white plumage, a rare trait among nocturnal predators, exploits the known aversion of rodents to bright light, explaining why, counterintuitively, moonlight has a lesser impact on the whitest owls. Our study provides evidence for the long-suspected influence of the Moon on the evolution of colouration in nocturnal species, highlighting the importance of colour in nocturnal ecosystems.

Colouration largely determines how animals interact with their biotic and abiotic environments[1]. Perception of an individual's colouration by conspecifics, predators and prey depends on the reflective properties of an individual's colour, its environmental background, the viewer's visual system and the environmental light[2,3]. The latter component might shape the evolution of colouration, with heterogeneous light conditions favouring distinct colourations, as shown, for instance, in African cichlid fish living at different depths[4,5] and in birds exploiting the canopy or the understory of tropical forests, inhabiting less or more cloudy environments, or nesting in the open or in dark tree cavities[6–8]. However, most of the studies linking variation in environmental light and organismal colouration come from diurnal species, and the consequences of variation in nocturnal light on the evolution of animal colouration are barely known[9].

The Moon has shadowed the evolution of life, which adapts its endogenous rhythms to the lunar cycle[10–14]. Moonlight alters the activity patterns of animals[15–18] because it alters an individual's capacity to visually detect food or to remain concealed[19–22]. By producing contrasting changes in light conditions[23], the Moon might also drive the evolution of colouration in nocturnal animals, but this hypothesis has received little attention despite being proposed more than one hundred years ago[24]. It is difficult to observe behaviour in nocturnal species[25], and in addition, some authors have suggested that our limited night vision has 'clouded' our expectations of the importance of colour and light variation for nocturnal species[26]. This could explain why the colouration of nocturnal species has often been considered to be an adaptation for diurnal camouflage rather than for a nocturnal life[27].

In line with the accumulation of studies highlighting the importance of colour vision in nocturnal species[23,28,29], a few recent studies have indirectly addressed how nocturnal light variation relates to animal colouration. Cuttlefish, *Sepia apama*, actively adapt their colour patterns to their background not only during the day, but also during the night[25,30]. Eagle owls, *Bubo bubo*, call more often during full-moon nights when their white throat patches, a potential visual signal[31], seem to be more consipicuous[32]. Colour polymorphism is more common in owls living in light-heterogeneous habitats formed by both forested and open landscapes[33]. Variation in nocturnal light levels might thus act as a selective agent on animal colouration. However, evidence supporting the notion that moonlight variation affects the fitness of individuals with respect to their colouration is still lacking.

By combining data from a breeding population monitored over the last 20 years with high-resolution global positioning system (GPS) tracking, we investigated how moonlight affects foraging, as well as the success and timing of breeding, in barn owls, in which genetic variation produces ventral plumage ranging from white to dark red[34,35] (Fig. 1). To identify the mechanism behind colour-specific performance in barn owls, we experimentally investigated the antipredator response of the barn owls' main prey, the common vole (*Microtus arvalis*), when exposed to white and red owls under different moonlight conditions. The adaptive role of the red and white plumage of barn owls remains unknown. Some previous studies have used genetic models to discard that colour variation in this species follows the expectation of a neutral trait[36,37], while other studies have suggested that colour variation may have a role in predator–prey dynamics[38,39]. Because light variation might affect the ability of prey to visually detect predators[10], we predict that moonlight influences owl hunting efficiency and, thereby, breeding success and timing. Rodent prey are likely to perceive different

---

[1]Department of Ecology and Evolution, University of Lausanne, Biophore Building, Lausanne, Switzerland. [2]Swiss Ornithological Institute, Sempach, Switzerland. [3]Lund Vision Group, Department of Biology, Lund University, Lund, Sweden. [4]FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa. *e-mail: luismsanjose@gmail.com; alexandre.roulin@unil.ch

Fig. 1 | Colour variation in barn owls. Barn owls exhibit continuous variation in plumage colouration, from white to dark reddish. Credit: Isabelle Henry

owl plumages as different shades of grey (that is, as differences in luminance), with the less-reflective plumage of red owls appearing darker than white plumage[40,41]. Similar to other vertebrates with duplex retinae, rodent prey probably rely on sensitive but colourless rod vision[28]. Even if some rodent species have up to two cone types[42] and might see colours, the rodents' chromatic vision, in addition to luminance, should make red owls appear less conspicuous than white owls. Thus, we expect that barn owls should be more conspicuous during full-moon nights and exhibit a lower foraging success. This negative effect of moonlight should be stronger in white than in red owls because white plumage is expected to reflect light more efficiently. We expect smaller differences during new-moon nights because limitation of dark noise in dim light is likely to result in less contrasted differences between red and white owls[28].

Results

Effect of plumage colouration and moonlight on food provisioning and hunting success. Using infrared cameras, we first investigated whether parental colour and moonlight (measured as the visible percentage of the Moon; see Methods and Supplementary Fig. 1) affect food provisioning (the total number of prey that adults brought to their offspring each night). On average, food provisioning was 4.78 prey per night ± 1.22 (standard error, s.e.) and was significantly associated with moonlight in interaction with parental colour (Poisson generalized linear mixed model (GLMM): $z = -2.33$, $P = 0.02$; Supplementary Table 1 and Fig. 2a). The food provisioning of the reddest parents decreased from new-moon (5.67 prey ± 1.21) to full-moon (3.27 prey ± 1.25; $z = -3.72$, $P < 0.001$) nights. There was no significant relationship between food provisioning and moonlight in the whitest parents ($z = -0.81$, $P = 0.42$), who brought 4.94 ± 1.21 and 4.61 ± 1.22 prey during new- and full-moon nights, respectively.

Hunting success, as measured in males equipped with GPS trackers, significantly depended on the interaction between plumage colouration, moonlight and hunting effort (Supplementary Table 2). We observed no effect of moonlight and plumage colouration on hunting success when owls performed a below-the-mean hunting effort (<26 hunting events per night, binomial GLMM: $z = 0.54$, $P = 0.588$). When the owls' effort was above the mean, hunting success in the reddest owls decreased from 0.48 ± 0.3 (s.e.) at new-moon nights to 0.42 ± 0.2 at full-moon nights (plumage colouration × moonlight: $z = -2.28$, $P = 0.023$, contrast within the reddest owls: $z = -2.34$, $P = 0.019$, Fig. 2b). No significant effect of moonlight was detected within the whitest owls ($z = 1.45$, $P = 0.147$, Fig. 2c). Owls do not adjust their hunting effort to moonlight or plumage colouration, but moonlight affected at which time of the night the owls hunted (Supplementary Table 3 and Supplementary Fig. 2).

Effect of plumage colouration and moonlight on prey anti-predator behaviour. To investigate why full- and new-moon light conditions have different effects on the parental food provisioning and hunting success of white and red owls, we experimentally investigated how common voles (the staple prey in our owl population[38]) detect and react (by either freezing or fleeing[43,44]) to red and white taxidermized barn owls under light conditions mimicking full- and new-moon nights (see Methods). Regardless of owl colouration, the probability of vole response to the owls was 0.49 ± 0.07 (s.e.) under the full-moon conditions and was significantly smaller at 0.20 ± 0.05 under the new-moon conditions (binomial GLMM: moonlight: $\chi^2 = 31.36$, degrees of freedom (d.f.) = 1, $P < 0.0001$, owl morph: $\chi^2 = 0.03$, d.f. = 1, $P = 0.862$, interaction: $\chi^2 = 0.58$, d.f. = 1, $P = 0.447$; Supplementary Table 4 and Fig. 3a).

Voles responded to the owls mainly by freezing (83% of the trials). The time they spent frozen was on average 9.5 sec ± 1.3 (s.e.), and the amount of time significantly depended on the interaction between owl colouration and moonlight (LMM: $t_{41.78} = 2.02$, $P = 0.049$, Supplementary Table 4). Under full-moon conditions, voles froze for 5.15 sec ± 1.6 longer when facing a white owl rather than a red owl ($t_{47.46} = 2.42$, $P = 0.039$), and voles froze for 9.6 sec ± 2.0 longer when facing a white owl under full-moon compared to new-moon conditions ($t_{47.41} = 3.59$, $P = 0.003$, Fig. 3b). No significant differences were found between white and red owls under new-moon conditions ($t_{39.50} = -1.10$, $P = 0.368$) or in response to red owls under full- and new-moon conditions ($t_{56.26} = 0.85$, $P = 0.424$).

To confirm that the increased freezing times observed were caused by the amount of light reflected from white plumage during full-moon conditions, we experimentally tested the prediction that voles should spend less time frozen after facing a white owl of reduced plumage reflectance. To test this, we masked the plumage reflectance of one mounted white owl by applying duck preen wax (CDC) to its feathers (see Methods, Fig. 3c). Under full-moon conditions, decreased plumage reflectance resulted in significantly shorter freezing times in voles (13.6 sec ± 1.2 (s.e.)) than those produced by white plumage without CDC (26.4 sec ± 1.2, LMM, moonlight $\chi^2_1 = 5.56$, $P = 0.018$, CDC treatment: $\chi^2_2 = 21.69$, $P < 0.001$, interaction: $\chi^2_2 = 21.24$, $P < 0.001$, contrast under full-moon conditions: $t_{24.05} = 4.66$, $P < 0.001$; Fig. 3d). No differences were found under new-moon conditions ($t_{6.21} = 1.35$, $P = 0.223$).

Effect of moonlight and parental colouration on nestling mass and survival. We investigated the potential fitness consequences of the effect of moonlight and plumage colouration by testing whether offspring body mass and fledging success reflect the effects observed in food provisioning. The offspring body mass depended on the moonlight in interaction with the father's colour (LMM: $\chi^2_1 = 4.49$, $P = 0.034$; Supplementary Table 5). Consistent with the patterns of food provisioning, the offspring mass decreased from new-moon (224.1 g ± 2.2 (s.e.), estimated at the mean nestling age (30 d)) to full-moon nights (220.7 g ± 2.3) in nests raised by the reddest fathers ($\chi^2_1 = 4.49$, $P = 0.04$, Fig. 4a,b). The body mass of owlets raised by the whitest males was not significantly different from new- to full-moon nights (228.0 g ± 1.5 and 228.8 g ± 1.5, respectively, $\chi^2_1 = 2.23$, $P = 0.13$). Thus, the major differences between colour morphs occurred during full-moon nights (6.6 g ± 1.0, $\chi^2_1 = 5.37$, $P = 0.021$) but not during new-moon nights (2.3 g ± 1.0, $\chi^2_1 = 0.36$, $P = 0.55$).

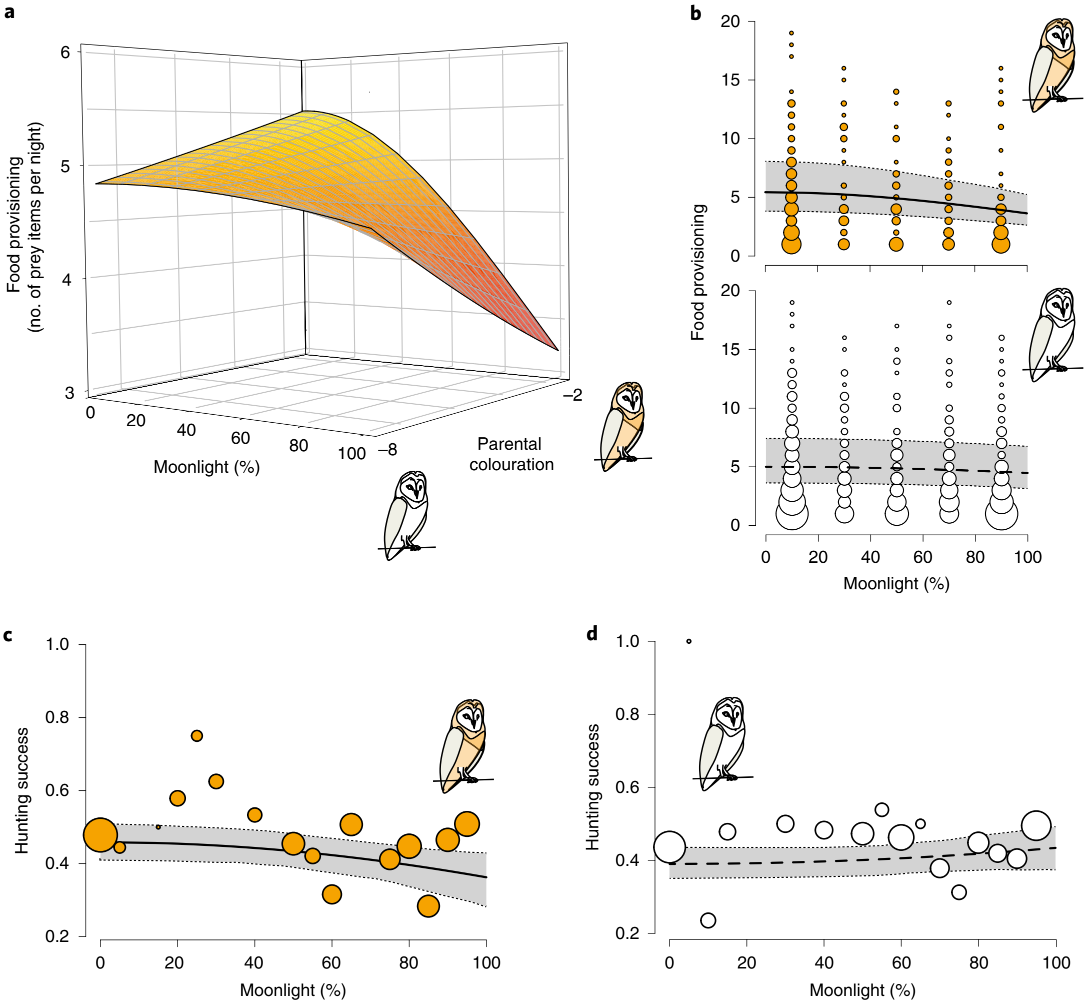


Fig. 2 | Parental food provisioning depends on moonlight and parental plumage colouration in the barn owl. a, Relationship between the total number of prey items brought by male and female parents and plumage colouration in interaction with moonlight. The predicted surface from a Poisson GLMM is presented. **b**, Detailed effects of moonlight on food provisioning. Shown are the observed values of food provisioning (pooled every 20 units of moonlight for clarity, with dot size proportional to the number of observations: smallest dots = 1 observation, largest dots = 77 observations), regression lines (continuous and dashed lines reflect significant and non-significant associations, respectively) and 95% confidence interval (grey shaded area) for barn owls above the third quantile (reddest owls) and first quantile (whitest owls) of colour variation. **c**,**d**, Hunting success within the reddest (**c**) and whitest owls (**d**). Shown are the observed values of hunting success (pooled every 5 units of moonlight for clarity, with dot size proportional to the number of observations: smallest dots = 1 observation, largest dots = 694), regression lines (continuous and dashed lines reflect significant and non-significant associations, respectively) and 95% confidence interval for barn owls above the third quantile (reddest owls) and first quantile (whitest owls) of colour variation.

We observed no effect of the moonlight and father plumage colour on fledging success (binomial GLMM: $\chi^2_1 = 0.04$, $P = 0.52$, Supplementary Table 6). However, due to a marked age hierarchy (rank) among barn-owl siblings, with first-born (high-rank) nestlings exhibiting highest survival probability (above 75%; Supplementary Fig. 3a), we expect the youngest nestlings to be more affected by reduced food provisioning. When only low-ranking offspring (rank ≥ 7) were considered, fledging success depended on the moonlight in interaction with father colouration (quasibinomial GLMM: $t_{62} = -2.58$, $P = 0.012$, Supplementary Table 7). From new- to full-moon nights, fledging success increased in nestlings raised by the whitest parents (from 0.35 ± 0.2 (s.e.) to 0.95 ± 0.1, $t_{62} = 3.03$, $P = 0.008$), while it tended to decrease in nestlings raised by the reddest parents (from 0.61 ± 0.3 to 0.14 ± 0.1, $t_{62} = -1.97$, $P = 0.071$; Fig. 4c,d). When accounting for cloud cover, which can mask moonlight effects (see Methods), the contrast remained significant for the whitest parents ($t_{61} = 3.65$, $P = 0.001$) and became significant for the reddest parents ($t_{55} = -2.09$, $P = 0.040$) (Supplementary Table 8).

Association between plumage colouration and moonlight and breeding. We observed a significant negative association between male colouration and the moonlight levels on the night a male's mate laid the first egg ($z = -2.87, P = 0.004$, Supplementary Table 9a). Females that mated with the whitest males had a higher probability of laying the first egg of their clutch (0.58 ± 0.02 (s.e.)) during nights with at least 50% of the Moon's surface illuminated, whereas females who mated with the reddest males had a higher probability of laying the first egg (0.62 ± 0.06) when less than 50% of the Moon's surface was illuminated (Fig. 5). Given the Moon cycle of roughly 29 d, we can expect similar negative associations between moonlight and plumage colouration at other moments of the barn owl's breeding cycle; more relevantly, when the first in-nest copulations are expected to occur (~27 d before laying the first egg[45], $z = -2.27$, $P = 0.023$), and when nestlings of rank 6–8 are expected to reach an age of 15 d old (between 59 and 63 d; roughly 2 moon cycles after a female laid the first egg: $z = -2.61, P = 0.009$, Supplementary Table 9b, c).

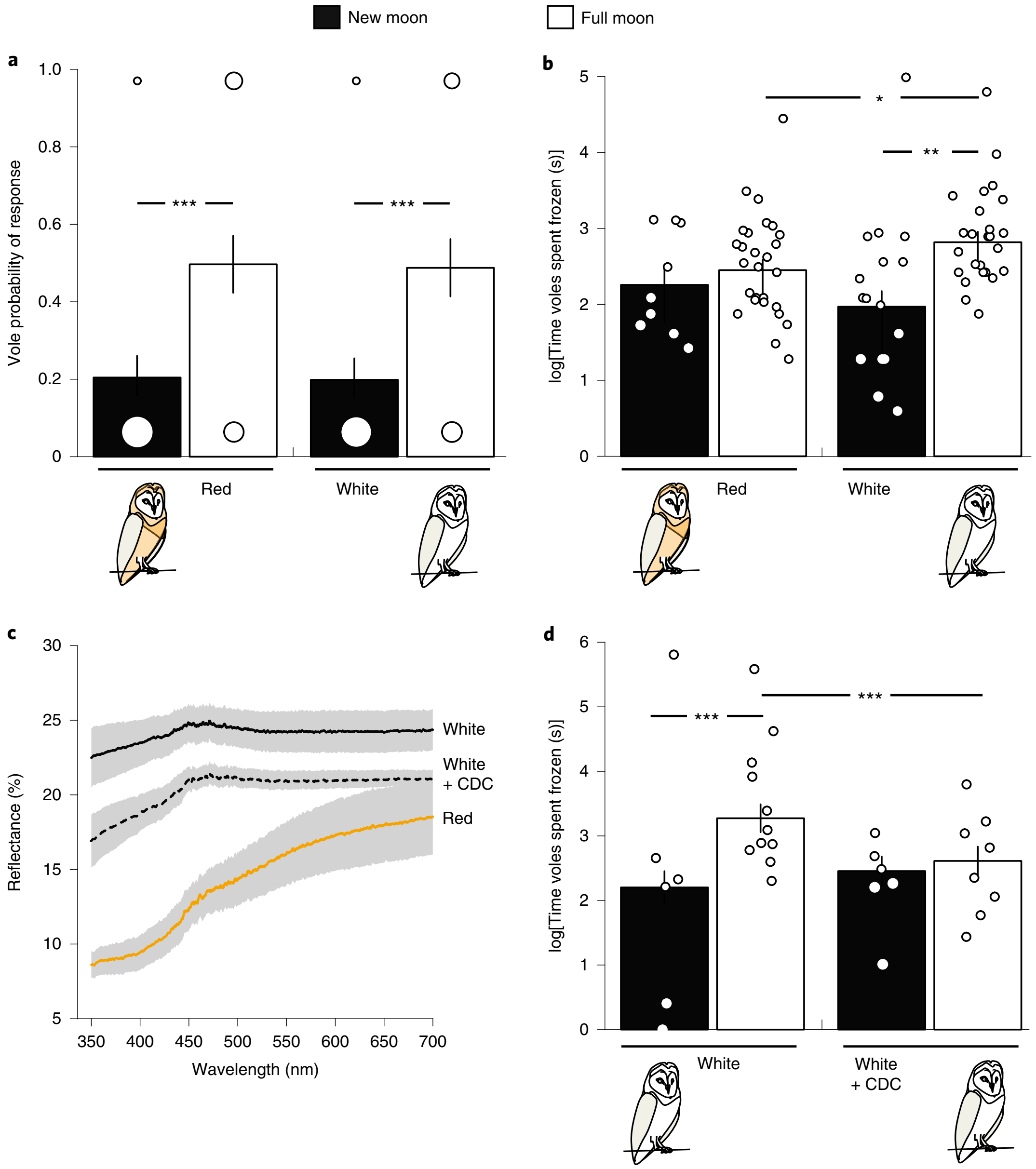


Fig. 3 | Probability of response and time spent frozen of common voles as a function of barn-owl plumage colouration and moonlight conditions. **a**, Probability (± s.e.m.) that common voles detected (and exhibited either freeze or flee behaviour) stuffed owls of white and red colour under light conditions mimicking full- and new-moon nights. The size of the white dots represents the number of observed responses of the voles (smallest dots = 21 observations, largest dots = 85 observations). **b**, Time (± s.e.m.) voles spent frozen (immobile) after observing white and red owls under light conditions mimicking full- and new-moon nights. **c**, Mean reflectance spectra (± s.e.m.) of the plumage of a white owl, a white owl treated with CDC wax and a red owl. **d**, Time (± s.e.m.) voles spent frozen (immobile) after observing a normally coloured white or a white owl treated with CDC under light conditions mimicking full- and new-moon nights. $^{***}P \leq 0.001$, $^{**}P \leq 0.01$, $^{*}P \leq 0.05$.

Discussion

Our study shows that the Moon differently affects the hunting performance and the reproductive success and timing of barn owls with contrasting plumage colourations. This supports the long-standing, untested hypothesis that moonlight influences colouration of nocturnal animals[9,24,30], particularly by uncovering a link between fitness proxies, moonlight and colouration that was missing in previous studies[25,32]. Moreover, our study raises the possibility that the unique white colouration of barn owls might be favoured by moonlight owing to the effect that the light being reflected from white plumage has on the prey's behaviour.

The reddest owls show diminished food provisioning and hunting success on full-moon nights (Fig. 2a,c). Lower hunting success and food provisioning of the reddest owls during full-moon nights can be explained by the higher probability of voles detecting owls under full-moon conditions (Fig. 3a). The effect of the moonlight on hunting performance has a mirroring effect on reproductive success. In owlets raised by the reddest owls, body mass decreases from new- to full-moon nights, in line with the reddest parents bringing more prey during new-moon nights than during full-moon nights. Consequently, the survival prospects of nestlings raised by the reddest parents were lower when maximal nestling growth occurred during full-moon nights (when owlets received less food and weighed less). Survival impairment was only evident in the youngest chicks (age rank ≥ 7), probably because their smaller size made them more vulnerable than their older siblings[46].

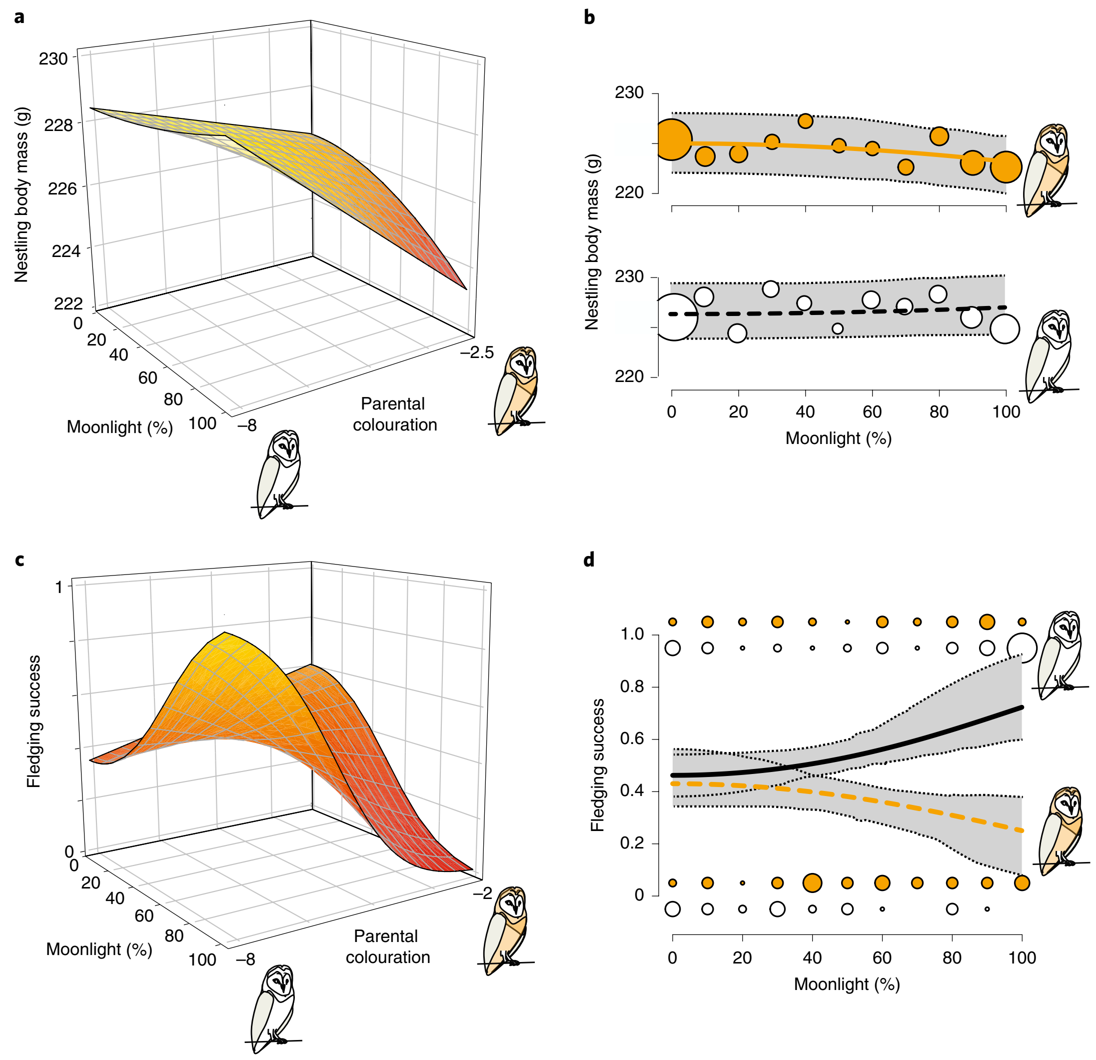


Fig. 4 | Offspring body mass and survival depend on moonlight and parental plumage colouration in the barn owl. a, Relationship between moonlight and father plumage colour and the effect on offspring body mass (predicted surface from a LMM). **b**, Detailed effects of moonlight on nestling body mass. Shown are the observed mean values of nestling body mass (pooled every 5 units of moonlight for clarity, with dot size proportional to the number of observations: smallest dots = 224 observations, largest dots = 993 observations), regression lines (continuous and dashed lines reflect significant and non-significant associations, respectively) and 95% confidence interval for barn owls above the 3rd quantile (reddest owls) and 1st quantile (whitest owls) of colour variation. **c**, Relationship between moonlight (at nestling age of 15 d) and father plumage colour for fledging success of low-rank owlets (rank ≥ 7). **d**, Relationship between fledging success of low-rank owlets and moonlight (at nestling age of 15 d) raised by the whitest fathers (plumage colour ≤ 1st quantile) and the reddest fathers (plumage colour ≥ 3rd quantile). Lines indicate the regression lines (continuous and dashed lines reflect significant and non-significant associations, respectively) and 95% confidence interval, and dots indicate the observed fledging success (pooled every 5 units of moonlight for clarity, with dot size proportional to the number of observations: smallest dots = 1 observation, largest dots = 8 observations).

Contrarily, food provisioning, hunting success and offspring body mass in the whitest owls were less or were not affected by moonlight (Figs. 2 and 4a,b). The whitest owls might actually perform better during full-moon nights, as suggested by the survival of their youngest nestlings raised being positively related to moonlight (Fig. 4c,d). In our population, the diet of both white and red owls is dominated by common voles, but white owls consume wood mice, *Apodemus* spp., more frequently than red owls[38]. However, differences in the diet associated with colouration are unlikely to drive the observed effects in our study because both *Apodemus* and *Microtus* show moon-avoidance behaviours[47–49].

Contrary to our expectations, plumage colouration did not affect the probability of voles detecting an owl (Fig. 3a). This suggests that white owls do not pay a higher cost of detectability than red owls (note that differences might still exist but went undetected in our study). However, there might be a benefit to white plumage in full-moon conditions as white plumage induces longer freezing times in rodents (Fig. 3b). Bright light is an aversive stimulus for rodents[50–53], and even small amounts of light (between 10^{-3} and 10^{-2} cm m^{-2} of luminance; that is, below the luminance of a full-moon night[23]) are aversive, at least in rats[54]. In fact, light is often used in neuroscientific studies to trigger freezing behaviour and to study the mechanisms of fear[55]. Given this fact, it is possible to interpret longer freezing times in voles attacked by a white owl as the result of a greater aversion to the light reflected by a white plumage. This is further supported by the lower freezing times that voles showed after masking the plumage reflectance of a white owl (Fig. 3c,d). This experiment showed that the amount of light reflected from the plumage was the factor influencing voles' freezing times.

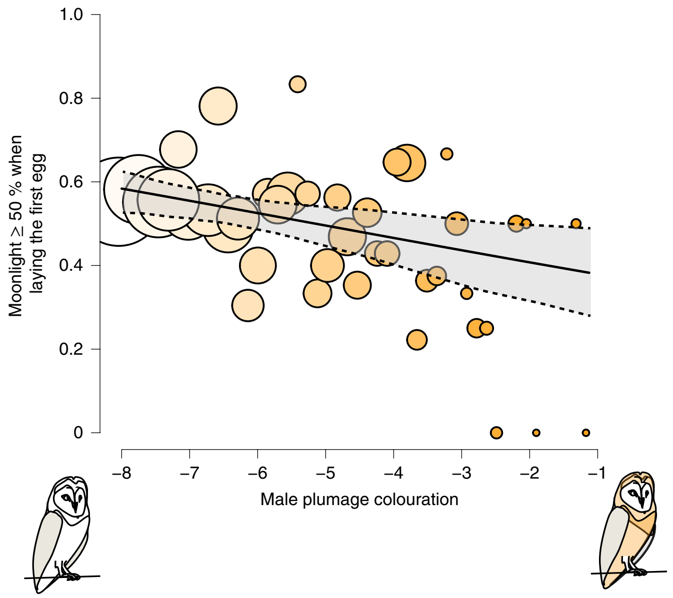


Fig. 5 | Plumage colouration in association with moonlight levels on the night females laid the first egg of a clutch. Probability that a female laid the first egg during nights with 50% or more of the Moon surface illuminated in relation to male plumage colouration. Shown are the observed proportions of cases (pooled every colour unit to the first decimal, smallest dots = 1, largest dots = 181), the regression line and the 95% confidence interval.

Inducing longer freezing times in prey can be adaptive for barn owls because a barn owl's hunting success substantially increases when prey stays immobile (up to 100% in laboratory conditions[43,44]). By exploiting sensory biases in the prey[56], white owls might enhance their hunting success during full-moon nights, explaining why moonlight had a smaller or no effect on food provisioning and hunting success of the whitest owls in comparison to the reddest owls. Whether the freezing responses of prey species others than common voles are also affected by the white barn owl plumage still needs to be assessed. Light aversion has been observed in mice of the genus *Mus* and in rats (*Rattus norvegicus*), so it is likely that other prey species common in the barn owl's diet, such as mice of the genus *Apodemus* (~20% of the barn owl's diet[38]), are also aversive to light and might respond to white and red plumage differently. Evidence supporting the notion that males make a larger hunting effort than females (this study) and are selected to have more immaculate plumages[57,58] suggests that a white colouration might have evolved by enhancing male hunting capacity.

Given the effect of moonlight, we would expect red males to be rare in our population. However, white colouration may incur costs that inhibit white males from becoming more frequent. White plumage might compromise camouflage during the day, particularly against harassing competitors, such as carrion crows (*Corvus corone*). There might also be added benefits of displaying a redder plumage, particularly under harsh conditions when a higher melanin content in feathers could increase protection against feather abrasion, humidity and/or cold temperatures[59]. Thus, the hunting-related benefits of white plumage may trade-off against survival to some extent. In this case, we expect white plumage to be less frequent in owls exerting lower hunting efforts, such as females and fledglings, which is in line with their, on average, redder plumage colouration[34,60,61]. We can then expect different selective agents inducing balancing selection on adult male colouration, which might maintain colour variation in this species, perhaps in combination with ontogenetic conflict within males and sexual antagonistic selection.

Small white patches are common among nocturnal species[9]. We predict that, as observed here, their ecological and evolutionary significance will be better understood when considering how their effect on fitness changes with varying moonlight levels. A question that remains open is whether selection exerted by moonlight is sufficiently strong to induce an evolutionary change in colouration. Here, we observed that moonlight acts on the total number of fledglings produced by males raising broods of at least seven owlets. This comprises 26.7% of the broods per year (Supplementary Fig. 3b), ranging from 8.3% to up to 48.5% depending on the year[62]. Thus, even though the fitness effect of the Moon is restricted to some individuals, it may affect a substantial part of the population and with particular strength in some years. Once they have fledged, the recruitment of nestlings in the local breeding population is not related to their rank in the brood (binomial GLMM: $\chi^2_1 = 0.37$, $P = 0.54$, mean recruitment: 15.73% ± 2.54), supporting the notion that the differences in the breeding success of red and white males generated by moonlight may persist after nestlings fledge and have evolutionary consequences. Nevertheless, we cannot yet discard that the high juvenile mortality (the major fitness component in our population[62]) finally hinders any evolutionary response to moonlight. Thus, studies integrating the effects that the Moon has inside and outside the breeding season are still needed to understand the evolutionary consequences of moonlight.

We observed that the Moon also influences breeding timing in barn owls of different plumage colouration (Fig. 5), suggesting that owls adjust their phenology to the Moon cycle. As observed in raptors exhibiting colour polymorphism[63], this effect is in line with owls having evolved mechanisms that minimize the negative impact of varying light conditions on their offspring. Thus, by laying their first egg during nights of lower moonlight levels, the period of maximal growth in the youngest nestlings of the reddest males will also occur during nights with low moonlight levels, which may help the reddest males to avoid the observed negative effects of high moonlight levels. Moonlight might also influence breeding timing because males might indirectly drive oviposition through courtship feeding[64]. Thus, the Moon might also determine the onset of reproduction by affecting the number of prey that males of different colouration offer during courtship. In line with this hypothesis, we observed that first in-nest copulations were also more likely to occur with higher and lower moonlight levels in the whitest and the reddest males, respectively. However, roughly 60% of the first in-nest copulations occur without courtship feeding in barn owls[45], suggesting that the Moon might have a smaller influence at this time.

In conclusion, our study shows that light variation associated with the Moon cycle exerts selection on the plumage colouration of a widespread nocturnal predator, the barn owl. Similar to the effect of varying diurnal light conditions[6,65], light variation during the night is also an important ecological factor in our understanding of the colouration of nocturnal species. Interestingly, our study provides evidence for the idea that white barn owls exploit sensory biases in their prey, which might enhance prey catchability and help white owls to buffer the negative effects of moonlight. In line with the increasing evidence supporting the existence of accurate colour vision in numerous nocturnal species[26,40], our study contributes the idea that colour is important in nocturnal systems. This raises the concern that light pollution has the potential to interfere with the evolutionary and ecological dynamics associated with colouration of nocturnal species, which deserves the attention of future studies.

Methods

Study site and species. The study area comprises 1,070 km^2 between the lakes of Neuchatel and Leman in western Switzerland. Since 1991, 360 nest-boxes installed in farms were regularly monitored for barn-owl clutches. Eggs are laid every 2–3 d and incubation starts with the first egg, resulting in a marked age hierarchy (rank) among nestlings due to asynchronous hatching. The nests were revisited at least 4 times to capture the adults and record offspring development until fledging (roughly 55 d old). We used a balance to weigh owlets to the nearest 0.01 g, and their ages were estimated on the basis of wing length, measured to the nearest 1 mm, soon after their hatching. An individual was considered to have successfully fledged if it survived until the age of 55 d. Fresh prey remnants (number and species) were recorded on every visit to the nests. Prey remnants are those prey items that were not consumed by the nestlings and/or the females before our visit and therefore do not directly reflect total parental food provisioning.

Moonlight and colour measurements. The plumage colouration of adults was scored on the breast, belly, flank and the underside of the wings using an eight-colour chip ranging from −8 (white) to −1 (dark reddish), a method that highly correlates with objective spectrophotometric measurements of brown chroma (the ratio of long-wavelength reflectance, R600–700 nm, over total reflectance, R300–700 nm, see ref. [61] for further details). The average colour of all body parts was used for the statistical analyses. Barn owls also present a varying number of dark spots on their ventral plumage that are subject to sexual selection[66]. Including plumage spottiness on the models did not alter the results of the study (Supplementary Table 10).

Moonlight was measured as the visible percentage of the Moon. Except for the analyses on hunting success, we used the Moon visible percentage when the Moon passed the meridian as a single moonlight value for each night. The nights that moonset occurred within 1 h following sunset or that moonrise occurred within 1 h before sunrise (that is, the Moon was not visible during most of the night) were assigned a value of zero. The analysis of hunting success was based on observations at specific time points of the night, and hence we obtained values of the visible percentage of the Moon at each specific time point. For the analyses on offspring body mass, we collected data on moonlight of the night prior to the capture of the nestlings. For the analyses on offspring survival, we collected data on the moonlight levels at the nestling age of maximal growth rate (15 d old, mass gain 14.3 g d^{-1}, Supplementary Fig. 4), which is when nestlings are more sensitive to reduced food provisioning (nestlings that did not survive to fledging received less prey at age 15 d than those that survived; $t_{36} = -2.86$, $P = 0.007$). For the analyses on the association between moonlight and breeding, we collected data on moonlight for the night the females laid the first egg (assessed on the basis of the developmental stage of the clutch at the first time we visited the nest). We also collected data on moonlight for the nights when the first in-nest copulations were expected to occur (27 d before the first egg was laid[45]) and for the nights when nestlings of rank 6–8 were expected to reach an age of 15 d (given 14 d between the 1st and the 7th egg are laid, plus 31 d of incubation, and 15 d after hatching).

All the moonlight data were obtained for a locality within the study area (Yverdon-les-Bains; 46° 46′ 44′′ N, 6° 38′ 24′′ E) using a Javascript library (MeeusJs) developed by F. Soldati (www.github.com; last access in November 2018). The visible percentage of the Moon was square-root transformed for all the statistical analyses as this transformation improves the association with night illumination (Supplementary Fig. 1). Because nights with intense cloud cover are likely to introduce error in the effect of moonlight measured as the visible percentage of the Moon, we repeated the analyses including cloudiness as a predictor whenever possible. The models were re-run while considering cloudiness (percentage of the moon covered by clouds), which might affect light variation during the night. Including cloudiness in the models did not qualitatively change the results unless indicated otherwise in the Results section.

Parental food provisioning, GPS tracking and hunting success. Food provisioning was measured using infrared cameras at a total of 131 nest boxes ($n = 1{,}154$ observations of 201 different parents) in 5 years (1997, 2001, 2005, 2006, 2016). During the years 1997, 2001, 2005, and 2016, we used infrared video cameras (CCTV miniature cameras, Active Media Concept, France) connected to a recorder (Monacor International, Germany) and, in 2016, we equipped the nests with motion-sensitive camera traps (HC500 Hyperfire, RECONYX, USA). Food provisioning was recorded between 21.5 and 5.5 h for 3.4 nights ± 2.4 (s.d.) per nest on average. From the videos and pictures, we counted the total number of prey items brought on each night by the male and female parents, which were previously captured and ringed on different legs to facilitate their identification in the videos and pictures (for further details, see ref. [67]).

We monitored the foraging behaviour of 34 breeding male barn owls in 2016 and 45 in 2017 using GPS trackers. We used GiPSy-5 GPS tags (Technosmart, Italy) that measured 30 × 20 × 10 mm with the battery. These were coupled with a 40-mm-long antenna. The tags weighed between 12 and 13 grams (less than 5% of an owl's body mass) and were attached as a backpack with a Teflon harness. Each tag collected location, time and speed over ground every 10 sec at night, from 30 minutes before dusk to 30 minutes after dawn, to ensure a complete measurement of the activity period. In 2016 and 2017, breeding males were captured at their nest sites when the oldest nestling was 19–34 d old (mean = 25.4; s.d. = 2.8), equipped with GPS tags and released at the capture site. Approximately 2 weeks later, the owls were recaptured at the nest site in order to recover the GPS tags with the data. The trackers recorded the spatial location of each owl for an average of 8.1 nights ± 2.6 s.d. per owl. Prior to any analysis, GPS data were pre-processed and filtered for aberrant positions based on either speed or location.

An expectation-maximization binary clustering (EMbC) algorithm[68] was applied to classify barn owl movement data into different behaviours. EMbC uses an unsupervised approach (that is, based on no previous classification of the data) to cluster location data based on speed and turning angle between locations. We were interested in describing three main behaviours: perching, commuting and hunting. Perching was defined as a stationary behaviour, characterized by null or low speed and a wide range of turning angles due to the GPS error. Commuting was defined as a rapid straight flight, characterized by high speeds and low turning angles, often displayed after a prey capture between the hunting grounds and the nest box. Lastly, hunting was characterized by a slow and sinuous flight, with low to medium speed and medium to high turning angles. For validation, the EMbC behavioural classification was compared with a visual classification performed on a random subsample of the whole dataset (20 individuals). The correspondence between EMbC and the visual classification was high: 92.7% on average (perching = 94.5% ± 2.3 s.e.; commuting = 91.1% ± 3.8 s.e.; hunting = 92.6% ± 4.9 s.e.). Therefore, we considered EMbC's classification as reliable.

After detecting each event when the owls were likely to be hunting ($n = 13{,}558$), we classified a hunting event as successful if the owl flew back to its nest immediately afterwards (that is, it commuted) or as unsuccessful, if the owl resumed hunting. Although this indirect measure of hunting success might include as successful those cases when males visit the nest without a prey item and might leave out cases when an owl hunts close to and from a perching site, we found a good correspondence between the mean prey delivery rate of males per night observed using infrared cameras (7.08 preys ± 3.52 s.d.) with that estimated using the GPS tracks (8.94 preys ± 5.31 s.d., exact Poisson test $P = 0.45$). Additionally, the observed mean hunting success (~0.41 ± 0.1 s.e.) is also within the range observed in a previous study measuring owl success in catching prey in captivity (0.42 ± 0.2 s.e.)[44]. Thus, we consider that our indirect measurement of success is a good proxy for real hunting success.

Behavioural experiments. We used common voles, *Microtus arvalis*, to investigate how prey react to barn owls of different plumage colouration and under different light conditions. Common voles are the staple prey in our owl population (~55% of the diet[38]), and the analysis of fresh vole remains found in the nests suggests that the number of voles that owls capture depends on the interaction between moonlight and the owls' colouration in the same way as described above for food provisioning ($z = 2.11$, $P = 0.035$; fewer voles as prey remains the day after a full-moon night than after a new-moon night in the reddest owls: $z = -1.98$, $P = 0.048$; no effect of Moon cycle on the number of voles as prey remains within the whitest owls: z = 1.46, P = 0.143, Supplementary Table 11 and Supplementary Fig. 5).

The voles were captured within the first 2 weeks of February 2015 ($n = 24$) and on the first 2 weeks of March 2016 ($n = 23$) using Longworth live traps in the surroundings of the University of Lausanne, Switzerland and were housed individually in plastic terraria (42.5 × 26.6 × 18.5 cm) at the animal facilities of the University of Lausanne, Switzerland. The room temperature and humidity were kept constant at 22 ± 1 °C and 50%, respectively. Food (rodent food pellets, seeds and apple pieces) and water were provided ad libitum. The terraria were equipped with a hiding place, and hay and sawdust served as the substrate. We left the voles to acclimate to the laboratory conditions for 10 d and recorded their behaviour to the different owl colour morphs and light conditions during days 11 and 12. On day 13, they were released at the exact location where they were captured.

On the night of day 11, the voles were moved to a dark room enclosed by black cloth (Supplementary Fig. 6a) and placed individually in a larger terrarium (80 × 35 × 40 cm) with new substrate mixed with a handful of the substrate from the rodent terrarium to minimize stress. The room was divided into three lines (2.80 m large, 2 m high and 1 m wide) by black cloths, and two terraria were placed at the end of each line (the sides of the terraria were covered with black paper to keep the voles from seeing each other). To measure the vole response to owl colour morphs, we used two white (plumage colour score of −8) and two red (plumage colour score of −2 and −3.25) owls that were taxidermized in a flying posture (Supplementary Fig. 6c). The owls were suspended 1.60 m above the ground with a transparent nylon string and remained hidden under a black cloth at the end of each line at the opposite end of the voles' terraria. Twenty minutes after the voles were placed in the large terraria, we opened the cloth hiding the owl and let the owl slide through a 2-m-long zipline that went down to the opposite end of the line, which is where the voles' terraria were placed (Supplementary Fig. 6b). The 2-m length of the zip-line was chosen because the antipredatory response of the only rodent species previously tested (the spiny mouse, *Acomys cahirinus*) against an attacking barn owl occurred mainly within a range of 0–2 m between the owl and the rodents[44]. The owls were moved backwards along the zip-line and released again 2 more times (which were separated by 5 minutes), simulating the multiple attacks that owls often perform on their prey[43,44].

For each vole, the same procedure was repeated after 1 h on the same night but with an owl of a different colour. On the following night, the procedure was repeated with a different light condition (that is, at the end of the experiment, each vole was exposed to owls of both colourations and under both light conditions). To mimic full-moon light conditions, we placed two halogen lights (470 lumen each) attached together in one side of the room and at a distance of 3 m (Supplementary Fig. 6b). Halogen lights have been successfully used in previous studies to trigger moon-dependent behaviours[14], given their spectral similarity to the moonlight[69,70]. The light source was separated from the rodents by several black cloths so that the light in the first line measured with a standard luxometer was 0.25 lux, equivalent to full-moon light conditions at temperate latitudes[71]. To mimic new-moon conditions, the halogen lights were turned off, resulting in values below the detection level of the luxometer (<0.001 lux). The order with which the treatment (that is, the colour of the taxidermized owl) and the light conditions were applied to each rodent were randomized but controlling that there were the same number of trials for each combination of treatment order and light conditions.

In 2016, we included an additional manipulation to test whether the effect observed on the voles' freezing times was dependent on the amount of light reflected from the owls' white plumage. We exposed the rodents to a white owl, also taxidermized in a flying posture and whose plumage colouration was treated with duck preen wax ('cul de canard', CDC, Petitjean Fishing Equipment, SA, Switzerland) in addition to the red and white owls used in 2015. CDC was gently applied with a brush (6 drops per cm^2 of plumage) and significantly decreased plumage reflectance within the ultraviolet and visible wavelength ranges (see Fig. 3c).

During the trials, vole behaviour was recorded with two infrared video cameras, one located within the terraria and another located in a position above the terraria. From the video footage, we determined whether the voles responded to the owls (by either freezing or fleeing) or not (that is, the voles' behaviour remained unaltered after owl presentation). The amount of time that each vole spent frozen (time between the voles froze and resumed their activity) was measured from the videos to the nearest second. Because we were interested in investigating the response of the voles in relation to owl colouration, all the observations where the voles' orientation made them unable to see the owls were excluded (49 % of the trials). The final mean number of observations per vole was 6.04 ± 2.23 (s.d.) and was not significantly related to the owl colouration, the light conditions or the repeated exposure to the owls (all $t_{23} < 0.97$, $P > 0.34$).

Statistical analyses. All statistical analyses were conducted with R 3.0.2 (R Core Team, Vienna, Austria). LMMs and GLMMs were fitted with the functions lmer and glmer, respectively, implemented in the package 'lme4'[72]. GLMMs on food provisioning as a Poisson response variable included the random effect of Parent ID to account for repeated measurements on the same parents over several nights, Brood ID to account for male and female parents provisioning the same brood and Year ID to account for interannual variability in prey abundance. Fixed factors included moonlight, plumage colouration of the parent and their interaction. The fixed effects of sex, brood size and their interaction, and egg-laying date (including quadratic effects to account for within-year variation in prey abundance) were also included. GLMMs on hunting success as a binomial response variable included the random effects of Male ID to account for repeated measurements taken on the same male over several nights, and of Night ID (nested in Male ID) to account for repeated measurements on the same male within the same night. Year was included as a fixed factor given that the study only covers two years of GPS tracking. Fixed factors included moonlight at the beginning of a hunting event, male plumage colouration, hunting effort (the number of times a male was observed hunting over a given night) and all two-way and the three-way interaction between these terms. Hunting effort was included in the models because it may affect hunting success owing to owl's fatigue when hunting many times over the same night or because effort can reflect how suitable the conditions for hunting were over a given night (for example, low efforts might reflect poor climatologic conditions). We considered hunting effort in interaction with plumage colouration (and moonlight) because plumage colouration might associate with differences in stamina[73] and with different tail and wing morphologies that might affect how red and white owls hunt under different conditions[74]. We also included the linear, quadratic and cubic effects of the time of each hunting observation, after visually detecting that hunting success strongly decays during dawn and dusk. As for the models on food provisioning, the fixed effects of brood size and the linear and quadratic effects of laying date were also included.

The statistical models on vole behaviour (GLMM on vole probability to detect an owl as a binary response and LMM on freezing time) included the random effects of vole ID to account for repeated measurements on voles (each vole faced the same treatment three consecutive times), session (each vole was tested in the two moonlight conditions and with the two owl morphs), lane to account for potential variation within the experimental room and block (each year, voles were captured and tested in the experimental setting in groups of 7–8 voles). Fixed effects included owl morph (red versus white), moonlight condition (full- versus new-moon) and their interaction. The fixed effect of year (two-levels factor) and its interaction with the other terms was included to account for the fact that the experiment was repeated in two separate years by different observers. Repetition was included to account for differences in the response between the first, second and third time the same owl was presented to the rodents. For the analysis of time spent frozen, mean times of the three repetitions were taken.

LMMs on nestling body mass (log-transformed) were conducted on a total of 18,735 records of offspring body mass collected for 3,878 nestlings born over the last 20 years in 814 different broods. The models included the random effects of owlet ID to account for repeated measurements of body mass on the same nestlings, including the random slopes for nestling age, age^2, age^3. The IDs of the brood in which nestlings were born and raised were included to account for the shared environment and origin of nestlings. The IDs of the foster parents were included to account for repeated breeding of the same parents across several years. Fixed effects included moonlight, father plumage colouration and their interaction, as well as the following factors, which are known to affect nestling body mass: age (up to the fourth power[75]), hour (up to the third power), laying date (linear and quadratic), brood size and rank within the brood hierarchy. We only considered the colouration of the father given the larger male hunting effort. Males alone feed both their offspring and female partners until the first-born owlet is 2–3 weeks old[46]. From this time onward, females leave to produce another clutch[76] or stay but hunt significantly less than males (the average number of prey per night for females was 3.79 ± 0.67 (mean ± s.e.) versus 7.08 ± 1.21 for males; $z = 9.38$, $P < 0.001$, Supplementary Table 1).

GLMMs on nestling survival as a binary response variable included the same random and fixed terms as for models on nestling body mass except for owlet ID (no replication in survival within individuals), age and hour. These models were conducted on data from 4,504 nestlings from 944 broods monitored in the last 20 years, whereas the analyses restricted to nestlings of rank ≥7 was conducted on 217 barn owl nestlings from 150 broods. The GLM initial full model on the survival of nestling of rank ≥7 show evidences of underdispersion, and we used a penalized likelihood approach (function glmmPQL, package 'MASS')[77].

To test for an association between male colouration and moonlight levels on the date females laid their first egg ($n = 1,293$ clutches raised by 631 different males between 1994 and 2017), we created a binomial variable considering whether moonlight was ≥50% or <50% on a given date. We then fit a GLMM with moonlight as a binary response and considered the random effects of Year and Male ID (to account for repeated observations on the same males), and the fixed effect of male colouration. The same approach was used but with consideration of moonlight levels on the date when the first in-nest copulations were expected to occur and on the date when a females' nestlings of rank 6 or more were expected to reach the age of 15 d old.

For all models, Cook's D values were computed from the models to assess the influence of the observations on model performance, and collinearity was assessed by calculating the variance inflation factor for each of the quantitative parameters in the models[77]. All full models were simplified by backward elimination of non-significant terms ($P > 0.1$), which provided qualitatively similar results as when using an information-based (AIC) approach[78] (Supplementary Table 12). For posterior contrasts on the interactions between colour and moonlight, we performed multiple 'simple slopes tests'[77] using the minimum and maximum values of colour and moonlight as conditional values. The P values from the contrast tests were adjusted to account for multiple testing using the Benjamini–Hochberg approach. Significance was set at 0.05 (two-tailed).

Ethics. The monitoring of barn owls was performed under the legal authorization of the 'Service vétérinaire du canton de Vaud', Switzerland. Barn owls were equipped with GPS devices under the authorization of the 'Service vétérinaire du canton de Vaud', Switzerland (Authorization VD2844.a and VD3213). The voles were captured under the permit 2154 of the Canton de Vaud, Switzerland, and the behavioural experiments were authorized by the 'Service vétérinaire du canton de Vaud', Switzerland (Authorization VD2934).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available at https://doi.org/10.6084/m9.figshare.c.4712765.v1. The GPS data used to assess hunting success is stored in Movebank (www.movebank.org) and accessible under the project named 'Barn owl (*Tyto alba*)' (Movebank ID 231741797).

Received: 22 June 2018; Accepted: 24 July 2019;

References

1. Cuthill, I. C. et al. The biology of color. *Science* **357**, eaan0221 (2017).
2. Endler, J. A. On the measurement and classification of color in studies of animal color patterns. *Biol. J. Linn. Soc.* **41**, 315–352 (1990).
3. Endler, J. A. & Mappes, J. The current and future state of animal coloration research. *Phil. Trans. R. Soc. Lond. B* **372**, 20160352 (2017).
4. Terai, Y. et al. Divergent selection on opsins drives incipient speciation in lake victoria cichlids. *PLoS Biol.* **4**, 2244–2251 (2006).
5. Seehausen, O. et al. Speciation through sensory drive in cichlid fish. *Nature* **455**, 620–627 (2008).

6. Tate, G. J., Bishop, J. M. & Amar, A. Differential foraging success across a light level spectrum explains the maintenance and spatial structure of colour morphs in a polymorphic bird. *Ecol. Lett.* **19**, 679–686 (2016).
7. Gomez, D. & Théry, M. Influence of ambient light on the evolution of colour signals: comparative analysis of a neotropical rainforest bird community. *Ecol. Lett.* **7**, 279–284 (2004).
8. Avilés, J. M., Pérez-Contreras, T., Navarro, C. & Soler, J. J. Dark nests and conspicuousness in color patterns of nestlings of altricial birds. *Am. Nat.* **171**, 327–338 (2008).
9. Penteriani, V., Delgado, M. & del, M. Living in the dark does not mean a blind life: bird and mammal visual communication in dim light. *Phil. Trans. R. Soc. B* **372**, 20160064 (2017).
10. Kronfeld-Schor, N. et al. Chronobiology by moonlight. *Proc. R. Soc. B* **280**, 20123088 (2013).
11. Skov, M. W. et al. Marching to a different drummer: crabs synchronize reproduction to a 14-month lunar-tidal cycle. *Ecology* **86**, 1164–1171 (2005).
12. Grant, R. A., Chadwick, E. A. & Halliday, T. The lunar cycle: a cue for amphibian reproductive phenology? *Anim. Behav.* **78**, 349–357 (2009).
13. Grau, E., Dickhoff, W., Nishioka, R., Bern, H. & Folmar, L. Lunar phasing of the thyroxine surge preparatory to seaward migration of salmonid fish. *Science* **211**, 607–609 (1981).
14. Dacke, M., Byrne, M. J., Scholtz, C. H. & Warrant, E. J. Lunar orientation in a beetle. *Proc. R. Soc. B* **271**, 361–365 (2004).
15. Eads, Da, Jachowski, D. S., Millspaugh, J. J. & Biggins, D. E. Importance of lunar and temporal conditions for spotlight surveys of adult black-footed ferrets. *West. N. Am. Nat.* **72**, 179–190 (2012).
16. Kotler, B. P., Brown, J., Mukherjee, S., Berger-Tal, O. & Bouskila, A. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proc. R. Soc. B* **277**, 1469–1474 (2010).
17. Watanuki, Y. Moonlight avoidance behavior in leach' s storm-petrels as a defense against slaty-backed gulls. *Auk* **103**, 14–22 (1986).
18. Clarke, J. A., Chopko, J. T. & Mackessy, S. P. The effect of moonlight on activity patterns of adult and juvenile prairie rattlesnakes (*Crotalus viridis viridis*). *J. Herpetol.* **30**, 192–197 (1996).
19. Cozzi, G. et al. Fear of the dark or dinner by moonlight? reduced temporal partitioning among africa's large carnivores. *Ecology* **93**, 2590–2599 (2012).
20. Daly, M., Behrends, P. R., Wilson, M. I. & Jacobs, L. F. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim. Behav.* **44**, 1–9 (1992).
21. Mougeot, F. & Bretagnolle, V. Predation risk and moonlight avoidance in nocturnal seabirds. *J. Avian Biol.* **31**, 376–386 (2000).
22. Orsdol, K. G. V. Foraging behaviour and hunting success of lions in queen elizabeth national park, uganda. *Afr. J. Ecol.* **22**, 79–99 (1984).
23. O'Carroll, D. C. & Warrant, E. J. Vision in dim light: highlights and challenges. *Phil. Trans. R. Soc. B* **372**, 20160062 (2017).
24. Verril, A. E. Nocturnal protective coloration of mammals, birds, fishes, insects, etc. *Am. Nat.* **31**, 99–103 (1897).
25. Hanlon, R. T. et al. Adaptable night camouflage by cuttlefish. *Am. Nat.* **169**, 543–551 (2007).
26. Warrant, E. Vision in the dimmest habitats on earth. *J. Comp. Physiol. A* **190**, 765–789 (2004).
27. Merilaita, S. & Tullberg, B. S. Constrained camouflage facilitates the evolution of conspicuous warning coloration. *Evolution* **59**, 38–45 (2005).
28. Kelber, A., Yovanovich, C. & Olsson, P. Thresholds and noise limitations of colour vision in dim light. *Phil. Trans. R. Soc. B* **372**, 20160065 (2017).
29. Parejo, D., Avilés, J. M. & Rodríguez, J. Visual cues and parental favouritism in a nocturnal bird. *Biol. Lett.* **6**, 171–173 (2010).
30. Warrant, E. J. Visual ecology: hiding in the dark. *Curr. Biol.* **17**, 209–211 (2007).
31. Penteriani, V., Delgado, MdelM., Alonso-Alvarez, C. & Sergio, F. The importance of visual cues for nocturnal species: eagle owls signal by badge brightness. *Behav. Ecol.* **18**, 143–147 (2007).
32. Penteriani, V., Delgado, MdelM., Campioni, L. & Lourenço, R. Moonlight makes owls more chatty. *PLoS ONE* **5**, e8696 (2010).
33. Passarotto, A., Parejo, D., Penteriani, V. & Avilés, J. M. Colour polymorphism in owls is linked to light variability. *Oecologia* **187**, 61–73 (2018).
34. Roulin, A. & Jensen, H. Sex-linked inheritance, genetic correlations and sexual dimorphism in three melanin-based color traits in the barn owl. *J. Evol. Biol.* **28**, 655–666 (2015).
35. San-Jose, L. M., Ducret, V., Ducrest, A. L., Simon, C. & Roulin, A. Beyond mean allelic effects: a locus at the major color gene MC1R associates also with differing levels of phenotypic and genetic (co)variance for coloration in barn owls. *Evolution* **71**, 2469–2483 (2017).
36. Antoniazza, S., Burri, R., Fumagalli, L., Goudet, J. & Roulin, A. Local adaptation maintains clinal variation in melanin-based coloration of european barn owls (*Tyto alba*). *Evolution* **64**, 1944–1954 (2010).
37. Antoniazza, S. et al. Natural selection in a post-glacial range expansion: the case of the colour cline in the European barn owl. *Mol. Ecol.* **23**, 5508–5523 (2014).
38. Roulin, A. Covariation between plumage colour polymorphism and diet in the barn owl *Tyto alba*. *Ibis* **146**, 509–517 (2004).
39. Charter, M., Peleg, O., Leshem, Y. & Roulin, A. Similar patterns of local barn owl adaptation in the middle east and europe with respect to melanic coloration. *Biol. J. Linn. Soc.* **106**, 447–454 (2012).
40. Kelber, A. & Roth, L. S. Nocturnal colour vision - not as rare as we might think. *J. Exp. Biol.* **209**, 781–788 (2006).
41. Osorio, D. & Vorobyev, M. Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proc. R. Soc. B* **272**, 1745–1752 (2005).
42. Jacobs, G. H. Evolution of colour vision in mammals. *Phil. Trans. R. Soc. B* **364**, 2957–2967 (2009).
43. Eilam, D. Die hard: a blend of freezing and fleeing as a dynamic defense—implications for the control of defensive behavior. *Neurosci. Biobehav. Rev.* **29**, 1181–1191 (2005).
44. Ilany, A. & Eilam, D. Wait before running for your life: defensive tactics of spiny mice (*Acomys cahirinus*) in evading barn owl (*Tyto alba*) attack. *Behav. Ecol. Sociobiol.* **62**, 923–933 (2008).
45. Durant, J. M., Gendner, J.-P. & Handrich, Y. Behavioural and body mass changes before egg laying in the barn owl: cues for clutch size determination? *J. Ornithol.* **151**, 11–17 (2010).
46. Roulin, A. Effects of hatching asynchrony on sibling negotiation, begging, jostling for position and within-brood food allocation in the barn owl, *Tyto alba*. *Evol. Ecol. Res.* **6**, 1083–1098 (2004).
47. Navarro-Castilla, Á. & Barja, I. Does predation risk, through moon phase and predator cues, modulate food intake, antipredatory and physiological responses in wood mice (*Apodemus sylvaticus*)? *Behav. Ecol. Sociobiol.* **68**, 1505–1512 (2014).
48. Schmidt, K. A., Manson, R. & Lewis, D. Voles competing with mice: differentiating exploitative, interference and apparent competition using patch use theory. *Evol. Ecol. Res.* **7**, 273–286 (2005).
49. Halle, S. Effect of extrinsic factors on activity of root voles, *Microtus oeconomus*. *J. Mammal.* **76**, 88–99 (1995).
50. Barker, D. et al. Brief light as a practical aversive stimulus for the albino rat. *Behav. Brain Res.* **214**, 402–408 (2010).
51. Lockard, R. B. Some effects of light upon the behavior of rodents. *Psychol. Bull.* **60**, 509–529 (1963).
52. Bourin, M., Petit-Demoulière, B., Nic Dhonnchadha, B. & Hascöet, M. Animal models of anxiety in mice. *Fundam. Clin. Pharmacol.* **21**, 567–574 (2007).
53. Trullas, R. & Skolnick, P. Differences in fear motivated behaviors among inbred mouse strains. *Psychopharmacology* **111**, 323–331 (1993).
54. Campbell, B. A. & Messing, R. B. Aversion thresholds and aversion difference limens for white light in albino and hooded rats. *J. Exp. Psychol.* **82**, 353–359 (1969).
55. Sousa, N., Almeida, O. F. X. & Wotjak, C. T. A hitchhiker's guide to behavioral analysis in laboratory rodents. *Genes Brain Behav.* **5**, 5–24 (2006).
56. Ryan, M. Sexual selection, receiver biases, and the evolution of sex differences. *Science* **281**, 1999–2003 (1998).
57. Ducret, V., Gaigher, A., Simon, C., Goudet, J. & Roulin, A. Sex-specific allelic transmission bias suggests sexual conflict at *MC1R*. *Mol. Ecol.* **41**, 4551–4563 (2016).
58. Roulin, A., Altwegg, R., Jensen, H., Steinsland, I. & Schaub, M. Sex-dependent selection on an autosomal melanic female ornament promotes the evolution of sex ratio bias. *Ecol. Lett.* **13**, 616–626 (2010).
59. Romano, A., Séchaud, R., Hirzel, A. H. & Roulin, A. Climate-driven convergent evolution of plumage colour in a cosmopolitan bird. *Glob. Ecol. Biogeogr.* **28**, 496–507 (2019).
60. San-Jose, L. M. et al. Effect of the *MC1R* gene on sexual dimorphism in melanin-based colorations. *Mol. Ecol.* **24**, 2794–2808 (2015).
61. Dreiss, A. & Roulin, A. 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. *Biol. J. Linn. Soc.* **101**, 689–704 (2010).
62. Altwegg, R., Schaub, M. & Roulin, A. Age-specific fitness components and their temporal variation in the barn owl. *Am. Nat.* **169**, 47–61 (2007).
63. Tate, G., Sumasgutner, P., Koeslag, A. & Amar, A. Pair complementarity influences reproductive output in the polymorphic black sparrowhawk *Accipiter melanoleucus*. *J. Avian Biol.* **48**, 387–398 (2017).
64. Brommer, J. E., Karell, P., Aaltonen, E., Ahola, K. & Karstinen, T. Dissecting direct and indirect parental effects on reproduction in a wild bird of prey: dad affects when but not how much. *Behav. Ecol. Sociobiol.* **69**, 293–302 (2015).
65. Galeotti, P., Rubolini, D., Dunn, P. O. & Fasola, M. Colour polymorphism in birds: causes and functions. *J. Evol. Biol.* **16**, 635–646 (2003).
66. Orlowski, J., Harmening, W. & Wagner, H. Night vision in barn owls: visual acuity and contrast sensitivity under dark adaptation. *J. Vis.* **12**, 1–8 (2012).
67. Roulin, A. & Dijkstra, C. Female- and male-specific signals of quality in the barn owl. *J. Evol. Biol.* **14**, 255–266 (2001).
68. Garriga, J., Palmer, J. R. B., Oltra, A. & Bartumeus, F. Expectation-maximization binary clustering for behavioural annotation. *PLoS ONE* **11**, e0151984 (2016).

69. Chakraborti, S. Verification of the Rayleigh scattering cross section. *Am. J. Phys.* **75**, 824–826 (2007).
70. Aubé, M., Roby, J. & Kocifaj, M. Evaluating potential spectral impacts of various artificial lights on melatonin suppression, photosynthesis, and star visibility. *PLoS ONE* **8**, e67798 (2013).
71. Foster, R. G. & Roenneberg, T. Human responses to the geophysical daily, annual and lunar cycles. *Curr. Biol.* **18**, 784–794 (2008).
72. Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. Fitting linear mixed-effects models using lme4. Preprint at https://arxiv.org/abs/1406.5823 (2014).
73. Béziers, P., Ducrest, A.-L., Simon, C. & Roulin, A. Circulating testosterone and feather-gene expression of receptors and metabolic enzymes in relation to melanin-based colouration in the barn owl. *Gen. Comp. Endocrinol.* **250**, 36–45 (2017).
74. Roulin, A. Linkage disequilibrium between a melanin-based colour polymorphism and tail length in the barn owl. *Biol. J. Linn. Soc.* **88**, 475–488 (2006).
75. Almasi, B. & Roulin, A. Signalling value of maternal and paternal melanism in the barn owl: implication for the resolution of the lek paradox. *Biol. J. Linn. Soc.* **115**, 376–390 (2015).
76. Béziers, P. & Roulin, A. Double brooding and offspring desertion in the barn owl *Tyto alba. J. Avian Biol.* **47**, 235–244 (2016).
77. Quinn, G. P. & Keough, M. J. *Experimental Design and Data Analysis for Biologists* (Cambridge Univ. Press, 2002).
78. Grueber, C. E., Nakagawa, S., Laws, R. J. & Jamieson, I. G. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* **24**, 699–711 (2011).

Acknowledgements

We thank P. Ducouret for setting the video system to record the voles' behaviour, J. Buser for his guidance and help in housing the voles in the animal facilities, I. H. Dufresnes for her help with the long-term barn owl database and for providing the picture in Fig. 1, P. Guillemin for helping prepare the data on adult food provisioning, P. Christe for giving us access to the Longworth live traps, K. Safi for helping us with the analysis of the GPS data and the people that have been involved in monitoring our barn-owl population over the last 20 years. We thank L. Keller, B. Milá and J. Delhaye for providing comments on early versions of the manuscript. We acknowledge funding from the Swiss National Science Foundation, ref. 173178, to A.R.

Author contributions

A.R., A.A. and L.M.S.-J. conceived and designed the study. A.R., P.B., B.A., R.S., K.S. and C.G. collected the field data on barn owls. R.S., K.S. and C.G. conducted the GPS-tracking study with contributions from P.B. and B.A. L.M.S.-J., C.J., A.Q. and A.O.-X. designed and conducted the behavioural experiments with voles. L.M.S.-J. conducted the statistical analysis with the contribution of R.S. L.M.S.-J. and A.R. wrote the paper, with major contributions from A.R., A.K., and R.S. and with input from all co-authors.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-0967-2.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to L.M.S.-J. or A.R.

nature research

Corresponding author(s): NATECOLEVOL-18064665C

Last updated by author(s): Jul 22, 2019

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Information about moonlight was obtained using a Javascript library (MeeusJs, Fabio Soldati, www.github.com, last access on May 2018)
Data analysis	R 3.0.2

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The GPS data is accessible at Movebank (www.movebank.org, Movebank ID 231741797). The rest of the data set is available from the corresponding authors upon reasonable request.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The study is both experimental and correlative. The correlative part is divided into 5 sections to study i. food provisioning of (male and female) adults (Observations = 1154, taken on 201 different adults from 131 nests), ii. hunting success in adult males (Observations = 13558 on 79 males followed on average across 8.07 nights, 2.65 S.D.), iii. nestling body mass (Observations = 18735 on 3878 nestlings from 814 different nests), iv. nestling survival (records on 4504 nestlings from 944 broods, 217 nestling from 150 broods for the analysis restricted to the youngest nestlings), v. moonlight levels during egg laying (1,293 clutches of 631 males). For all this sections, the main predictors were moonlight (% of the Moon visible) and adult (both male and female) plumage coloration (i) and parent plumage coloration (ii) and the interaction between moonlight and plumage coloration. For v., only male plumage coloration was considered as the main predictor. The data of all these sections is hierarchical to a different extent depending on the analysis, as described in the tables of the supplementary material and in the methods section. The experimental part of the study was conducted following a repeated-measures design where factor levels (Moonlight and Owl coloration) were applied up to 3 times and following a crossed design to all the experimental units (47 common voles).
Research sample	The research sample for the correlative part is from a population of adult and nestling barn owls, Tyto alba, breeding in nest boxes in Western Switzerland. The sample size is determined by the number of breeding couples encountered each year. For the experimental part, we sample common voles, Microtus arvalis, inhabiting the surroundings of the campus of the University of Lausanne, Switzerland. The sample size for this part was determined after a preliminary power study.
Sampling strategy	Barn owls were sampling by visiting the nest boxes periodically during the breeding season. Sample sizes involving barn owls were determined by the number of breeding couples present in a year. A post-hoc power analysis (based on 1000 simulations of the dependent variable based on final model estimates, "simulate" function in R v.3.0.2, package lme4) indicates that power to detect the reported effects given the sample size was > 0.80. Voles were captured using traps placed at different sites of the campus of the University of Lausanne, Switzerland. The sample size for this part was determined after a preliminary power study using the "pwr" package of R v.3.0.2.
Data collection	Data on plumage colouration of adults was scored using an eight-colour chip ranging from -8 (white) to -1 (dark reddish), a method that highly correlates with objective spectrophotometric measurements. Depending on the year, it was recorded by Alexandre Roulin, Robin Sechaud, Paul Bezier or Betina Almasi. Data on the moonlight was obtained by Luis M. San-Jose for a locality within the study area (Yverdon-les-Bains; 46°46’44’’ N, 6° 38’24’’ E) using a Javascript library (MeeusJs) developed by Fabio Soldati (www.github.com, last access on May 2018). Data on food provisioning was measured by Alexandre Roulin, Robin Sechaud, and Betina Almasi using sensitive infrared video cameras (years 1997, 2001, 2005, and 2016) or camera traps (2016). Data on hunting success was measured from GPS location data using GiPSy-5 GPS tags mounted on the owls by Robin Sechaud, Kim Schalcher, and Charlène Gémard. The data was processed by Robin Sechaud using an Expectation-Maximization binary Clustering. Data on nestling body mass (measured using a balance to the nearest 0.01 g) and survival before fledging was obtained by Alexandre Roulin, Robin Sechaud, Paul Bezier and Betina Almasi. Data on vole antipredatory response was obtained by Luis M. San-Jose from the footage recorded by two infrared video cameras, one located within the terrarium of each rodent and another located in a position above the terrarium of each rodent.
Timing and spatial scale	Data on plumage coloration, nestling body mass and survival has been continuously recorded since 1991 during the breeding period (February-October). Food provisioning was monitored during the years 1997, 2001, 2005 and 2016 as part of different studies. Hunting success was recorded during 2016 and 2017. Rodent behavior was experimentally tested during the years 2015 and 2016. The spatial scale is local (Western Switzerland for barn owl data, campus of the University of Lausanne for the vole data).
Data exclusions	No observations were excluded expect for the experimental study. As we indicate in the methods:"Because we were interested in investigating the response of the voles in relation to owl coloration, all the observations where the voles’ orientation made them unable to see the owls were excluded (49 % of the trials)."
Reproducibility	The rodent experiment was conducted on two separate years with the same findings (Year has no interactive effect with the experimental factors, see Supplementary Table 4).
Randomization	Randomization was applied to allocate the order of the treatments (moon condition and owl coloration) to the voles (all the treatments were applied to all the voles).
Blinding	Most of the data was collected before starting this study and was therefore blind to Moon conditions. Data collection from the videos of the experiment with voles could not be done blindly in relation to the Moon conditions as this is visible on the videos. However, this data was collected blindly in relation to the plumage coloration of the stuffed owls. No blinding was used during the data analysis.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Not recorded

Location	The study area comprises 1,070 km2 between the lakes of Neuchatel and Leman in Western Switzerland.
Access and import/export	All the authorizations to capture and manipulate the animals used in the study were given by the 'Service vétérinaire du canton de Vaud' (Switzerland). All the pertinent permits are reported in the Methods section.
Disturbance	To the best of our knowledge, the study cause no mayor disturbances on the barn owls or the voles. We minimize the duration of the visits to the owls' nests, the size of the GPS tags, and the number of days the voles were kept in the laboratory.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	The study did not involve laboratory animals.
Wild animals	Adult and nestling barn owls, Tyto alba, of both sexes, that were captured in nest boxes either by hand or with the help of a net at the entrance of the nest. The owls were not transported to the laboratory but released in their nest immediately after manipulating them. Adult common voles, Microtus arvalis, of both sexes were caught in the field using traps and released in the location they were captured after the experiments.
Field-collected samples	The study did not involve samples collected on the field.
Ethics oversight	Veterinary service of the Canton of Vaud, Switzerland.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

nature ecology & evolution

SUPPLEMENTARY INFORMATION
https://doi.org/10.1038/s41559-019-0967-2

Differential fitness effects of moonlight on plumage colour morphs in barn owls

Luis M. San-Jose[1*], Robin Séchaud[1], Kim Schalcher[1], Clarisse Judes[1], Anastasia Questiaux[1], Aymeric Oliveira-Xavier[1], Charlène Gémard[1], Bettina Almasi[2], Paul Béziers[1], Almut Kelber[3], Arjun Amar[4] and Alexandre Roulin[1*]

[1]Department of Ecology and Evolution, University of Lausanne, Biophore Building, Lausanne, Switzerland. [2]Swiss Ornithological Institute, Sempach, Switzerland. [3]Lund Vision Group, Department of Biology, Lund University, Lund, Sweden. [4]FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa. *e-mail: luismsanjose@gmail.com; alexandre.roulin@unil.ch

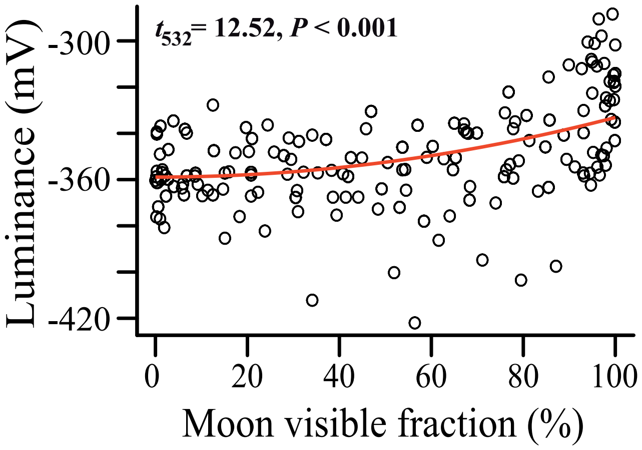
Supplementary information for

Differential fitness effects of moonlight on plumage colour morphs in barn owls

Luis M. San-Jose[1*], Robin Séchaud[1], Kim Schalcher[1], Clarisse Judes[1], Anastasia Questiaux[1], Aymeric Oliveira-Xavier[1], Charlène Gémard[1], Bettina Almasi[2], Paul Béziers[1], Almut Kelber[3], Arjun Amar[4], Alexandre Roulin[1*]

[1]*Department of Ecology and Evolution, University of Lausanne, Biophore Building, CH-1015 Lausanne, Switzerland;* [2]*Swiss Ornithological Institute, CH-6204 Sempach, Switzerland;* [3]*Lund Vision Group, Department of Biology, Lund University, Lund, Sweden;* [4]*FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa.*

*Correspondence: luismsanjose@gmail.com (L.M.S.-J.), alexandre.roulin@unil.ch (A.R.)



Supplementary Figure 1 | Relationship between the percentage of the Moon visible and night luminance values in the study area. Data on luminosity was obtained from a meteorological station (MeteoSwiss) located at the centre of the study area (Yverdon-les-Bains; 46°46’44’’ N, 6°38’24’’ E). The squared-values of moon visible fraction were used in the analysis given that they fit better the luminance values than a linear relationship.

Supplementary Table 1 | Effect of moonlight and parental plumage colouration on parental food provisioning in the barn owl. Poisson generalized linear mixed model of the total number of prey items provided by each parent for each night measured in 131 nests (N = 1,154 observations of 201 different parents). The full model was simplified by backward elimination of non-significant ($P > 0.1$) interactions (terms included in the final model are highlighted in bold). The final model's marginal $R^2 = 0.16$, conditional $R^2 = 0.62$.

Random effects

Parameter	**χ^2 (d.f.)**	***P***	**Variance**	**% Variance Explained**
Parent ID (*Intercept*)	101.34 (1)	< 0.001	0.081	11.08
Brood ID (*Intercept*)	55.71 (1)	< 0.001	0.075	10.38
Year (*Intercept*)	61.27 (1)	< 0.001	0.147	24.48

Fixed effects

Parameter	**Estimate* ± s.e.**	***z*-test**	***P***
Intercept	**1.24 ± 0.19**	**6.56**	**<0.001**
Brood size	**0.11 ± 0.04**	**2.52**	**0.012**
Sex**	**0.60 ± 0.06**	**9.38**	**<0.001**
Brood size × Sex**	**-0.10 ± 0.05**	**-2.14**	**0.032**
Laying date	**0.52 ± 0.29**	**1.81**	**0.071**
Laying date^2	**-0.55 ± 0.30**	**-1.82**	**0.069**
Moonlight	**-0.09 ± 0.02**	**-4.43**	**<0.001**
Plumage colour	**-0.01 ± 0.03**	**-0.23**	**0.819**
Moonlight × Plumage colour	**-0.04 ± 0.02**	**-2.33**	**0.020**
Sex** × Moonlight	-0.05 ± 0.04	-1.23	0.218
Sex** × Plumage colour	-0.09 ± 0.07	-1.31	0.189
Sex** × Moonlight × Plumage colour	0.05 ± 0.05	1.00	0.315

* Estimates based on standardized variables and a log link.

** Sex effects are given as male minus female estimates.

Supplementary Table 2 | Effect of moonlight and plumage colouration on hunting success in male barn owls. Results from a binomial generalized linear mixed model on the hunting success of 79 males over several nights (average number of nights: 8.07 ± 2.65 S.D., total number of observations: 13,558). Terms included in the final model are highlighted in bold. The model's marginal $R^2 = 0.011$, conditional $R^2 = 0.050$.

Random effects

Parameter	**χ^2 (d.f.)**	***P***	**Variance**	**% Variance Explained**
Male ID (*Intercept*)	66.2 (1)	< 0.001	0.078	2.56
Night ID in Male ID (*Intercept*)	20.8 (1)	< 0.001	0.057	1.63

Fixed effects

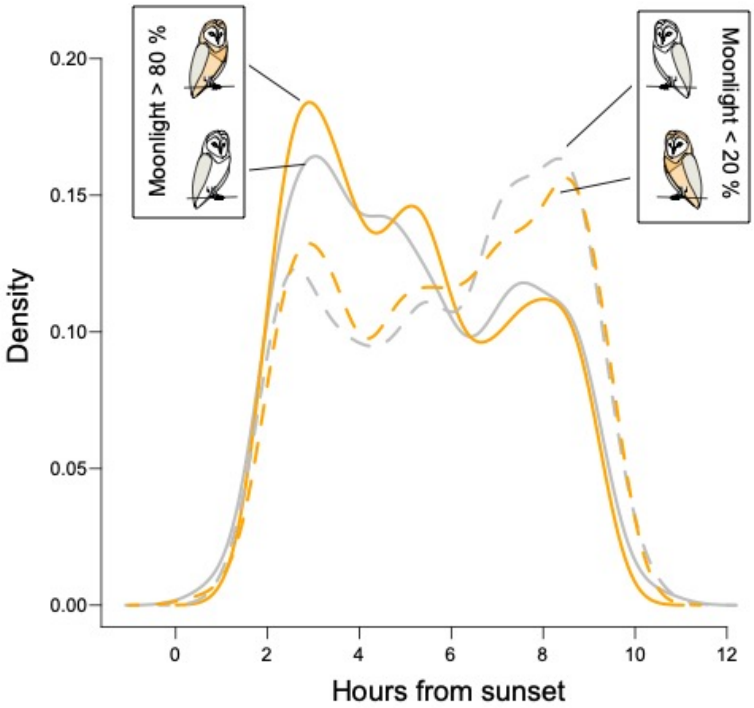
Parameter	**Estimate* ± s.e.**	***z*-test**	***P***
Intercept	**-0.347 ± 0.042**	**-8.26**	**<0.001**
Brood size	**0.040 ± 0.041**	**0.96**	**0.338**
Laying date	**-0.413 ± 0.243**	**-1.7**	**0.089**
Laying date^2	**0.377 ± 0.238**	**1.59**	**0.113**
Time of observation	**-20.13 ± 7.925**	**-2.54**	**0.011**
Time of observation^2	**41.01 ± 15.92**	**2.58**	**0.010**
Time of observation^3	**-21.06 ± 8.02**	**-2.63**	**0.009**
Year	**0.008 ± 0.046**	**0.16**	**0.871**
Hunting effort	**-0.002 ± 0.024**	**-0.08**	**0.938**
Plumage colour	**0.018 ± 0.043**	**0.42**	**0.671**
Moonlight	**-0.029 ± 0.029**	**-1.02**	**0.308**
Plumage colour × Moonlight	**-0.052 ± 0.028**	**-1.86**	**0.063**
Plumage colour × Hunting effort	**0.034 ± 0.023**	**1.49**	**0.137**
Moonlight × Hunting effort	**0.011 ± 0.023**	**0.47**	**0.636**
Plumage colour × Moonlight × Hunting effort	**-0.056 ± 0.023**	**-2.39**	**0.017**

* Estimates based on standardized variables and a logit link

Supplementary Table 3 | Effect of moonlight and plumage colouration on number of hunting events per night and on the time at which owls hunted. On the left, results from a quasi-Poisson generalized linear mixed model on the number of hunting events of 79 males over several nights (average number of nights: 8.07 ± 2.65 S.D., total number of observations: 638) (Model's marginal $R^2 = 0.03$, conditional $R^2 = 0.48$). On the right, results from a general linear mixed model on the time at which owls were observed hunting each night (average number of nights: 8.07 ± 2.65 S.D., total number of observations: 13,558) (Model's marginal $R^2 = 0.01$, conditional $R^2 = 0.15$). Terms included in the final models are highlighted in bold.

	Number of hunting events		Hunting time	
Random effects				
Parameter	**Variance (± 95 % IC)**	**% Variance Explained**	**Variance**	**% Variance Explained**
Male ID (*Intercept*)	0.04 (± 0.25)	1.10	<0.01	0.03
Night ID in Male ID (*Intercept*)	-	-	0.74***	4.54
Fixed effects				
Parameter	***t* (d.f.)**	***P***	***t* (d.f.)**	***P***
Intercept	**-0.97 (558)**	**0.333**	**603.35 (48.8)**	**<0.001**
Brood size	**1.02 (73)**	**0.311**	**2.16 (44.8)**	**0.036**
Laying date	**-0.64 (73)**	**0.522**	**0.52 (46.7)**	**0.606**
Laying date^2	**0.69 (73)**	**0.488**	**-0.27 (48.5)**	**0.790**
Year	**0.99 (73)**	**0.324**	**-2.88 (52.4)**	**<0.001**
Plumage colour	**0.50 (73)**	**0.618**	**-0.12 (45.6)**	**0.908**
Moonlight	**0.11 (558)**	**0.912**	**-7.70 (616.3)**	**<0.001**
Plumage colour × Moonlight	-1.25 (557)	0.213	**-1.89 (636.4)**	**0.059**

Supplementary Figure 2 | Effect of moonlight and plumage colouration on the time at which owls hunted every night. As moonlight increases, owls hunted more often at the beginning of the night and more often at the end of the night as moonlight decreases (see Table S3). Shown are the distribution of the time (hours from sunset) at which owls were observed hunting. Continuous grey and orange lines depict the distribution for the whitest and reddest owls when more than 80% of the Moon was illuminated. Dashed grey and orange lines depict the distribution for the whitest and reddest owls when less than 20% of the Moon was illuminated.



Supplementary Table 4 | Response of common voles (*Microtus arvalis*) to stuffed white and red barn owls under conditions mimicking full- and new-moon nights. The results from a binomial-GLMM on the probability that a vole detects an owl and a LMM on the time voles spent frozen (*i.e.*, immobile) after seeing an owl is presented. Random effects found significant by a likelihood-ratio test are indicated with an asterisk. The full models were simplified by backward elimination of non-significant ($P > 0.1$) interactions (terms included in the final model are highlighted in bold). For the model on the "probability to detect the owl" marginal $R^2 = 0.17$, conditional $R^2 = 0.26$. For the model on the "time spent frozen after seeing an owl" marginal $R^2 = 0.06$, conditional $R^2 = 0.09$.

	Probability to detect the owl		Time spent frozen after seeing an owl	
Random effects				
Parameter	**Variance**	**% Variance Explained**	**Variance**	**% Variance Explained**
Vole ID	0.157	3.52	0.031*	4.17
Session	0.192*	4.32	<0.001	<0.01
Block	<0.001	<0.01	0.003	0.48
Lane	0.026	0.58	<0.001	<0.01
Fixed effects				
Parameter	**χ^2 (d.f.)**	***P***	***t* (d.f.)**	***P***
Intercept	**5.26 (1)**	**0.022**	**16.43 (8.7)**	**<0.001**
Repetition	**2.26 (2)**	**0.323**	**-**	**-**
Owl morph	**0.03 (1)**	**0.862**	**2.42 (47.5)**	**0.016**
Moonlight condition	**31.36 (1)**	**<0.001**	**-0.80 (56.3)**	**0.420**
Year	**5.26 (1)**	**0.022**	**3.71 (2.76)**	**<0.001**
Owl morph × Moonlight condition	0.58 (1)	0.447	**-2.02 (47.5)**	**0.049**
Owl morph × Year	1.04 (1)	0.308	0.01 (47.8)	0.989
Moonlight condition × Year	0.01 (1)	0.969	1.01 (45.1)	0.313
Owl morph × Moonlight condition × Year	0.21 (1)	0.643	-0.08 (39.0)	0.939

Supplementary Table 5 | Effect of moonlight and father plumage colouration on offspring body mass in the barn owl. Results from a linear-mixed model on 18,735 measurements of body mass (log-transformed) of nestlings (*N* = 3,878) from 814 broods. Model's marginal $R^2 = 0.365$, conditional $R^2 = 0.99$. Terms included in the final model are highlighted in bold.

Random effects

Parameter	**χ^2 (d.f.)**	***P***	**Variance (100x)**	**% Variance Explained**
Owlet ID (*Intercept*)	1097.8 (1)	<0.001	0.35	0.23
Owlet ID (*Slope Age*)	1490.6 (1)	<0.001	15.7	10.28
Owlet ID (*Slope Age*^{2})	977 (2)	<0.001	62.1	40.62
Owlet ID (*Slope Age*^{3})	900.5 (3)	<0.001	17.5	11.42
Brood born (*Intercept*)	44.3 (1)	<0.001	0.09	0.06
Brood raised (*Intercept*)	29.2 (1)	<0.001	0.12	0.08
Foster father ID (*Intercept*)	0 (1)	1	0	0.00
Foster mother ID (*Intercept*)	3.2 (1)	0.072	0.02	0.01
Year (*Intercept*)	65.9 (1)	<0.001	0.06	0.04

Fixed effects

Parameter	**Estimate* ± s.e.**	**χ^2 (d.f. =1)**	***P***
Intercept	**5.401 ± 0.006**	**712390.0**	**<0.001**
Sex**	**0.037 ± 0.003**	**188.2**	**<0.001**
Laying date	**-0.017 ± 0.002**	**48.5**	**<0.001**
Age	**3.949 ± 0.017**	**51242.0**	**<0.001**
Age^2	**-7.639 ± 0.059**	**16522.0**	**<0.001**
Age^3	**6.169 ± 0.075**	**6696.8**	**<0.001**
Age^4	**-1.894 ± 0.033**	**3315.8**	**<0.001**
Brood Size	**0.012 ± 0.002**	**52.4**	**<0.001**
Rank within brood hierarchy	**-0.028 ± 0.001**	**514.3**	**<0.001**
Hour	**0.075 ± 0.007**	**106.2**	**<0.001**
Hour^2	**-0.172 ± 0.018**	**87.6**	**<0.001**
Hour^3	**0.079 ± 0.012**	**43.7**	**<0.001**
Father plumage colour	**-0.004 ± 0.002**	**3.4**	**0.070**
Moonlight	**-0.001 ± 0.001**	**0.5**	**0.535**
Moonlight × Father plumage colour	**-0.002 ± 0.001**	**4.5**	**0.033**

* Estimates based on standardized variables and the log transformation of juvenile body mass.

** Sex effects are given as male minus female estimates.

Supplementary Table 6 | Effect of moonlight and father plumage colouration on fledging success. Results from a binomial generalized linear mixed model on the fledging success of 4,504 nestlings (944 broods). The full model was simplified by backward elimination of non-significant ($P > 0.1$) interactions (terms included in the final model are highlighted in bold). Model's marginal $R^2 = 0.153$, conditional $R^2 = 0.743$.

Random effects

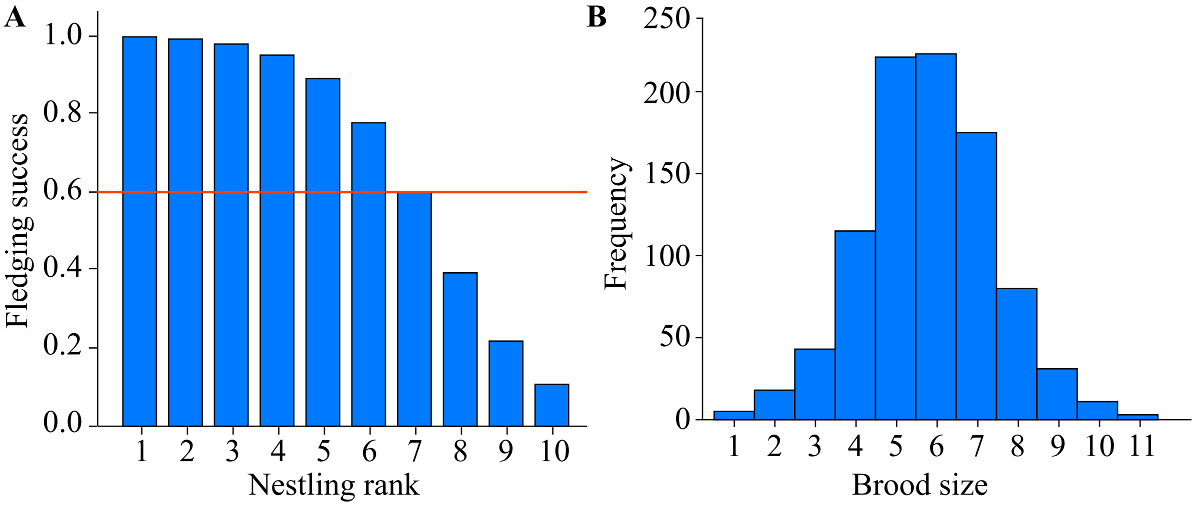
Parameter	**χ^2 (d.f.)**	***P***	**Variance**	**% Variance Explained**
Brood born (*Intercept*)	1.32 (1)	0.251	0.43	3.35
Brood raised (*Intercept*)	26.73 (1)	<0.001	3.68	28.80
Foster father ID (*Intercept*)	0.45 (1)	0.491	0.29	2.28
Foster mother ID (*Intercept*)	0.37 (1)	0.543	0.30	2.35
Year (*Intercept*)	99.14 (1)	<0.001	2.84	22.25

Fixed effects

Parameter	**Estimate* ± s.e.**	**χ^2 (d.f. =1)**	***P***
Intercept	**4.39 ± 0.46**	**91.69**	**<0.001**
Sex**	**0.15 ± 0.14**	**1.14**	**0.286**
Laying date	**2.00 ± 0.09**	**4.44**	**0.035**
Laying date^2	**-2.38 ± 0.92**	**6.69**	**0.010**
Brood size	**0.64 ± 0.13**	**25.05**	**<0.001**
Rank within brood hierarchy	**-1.41 ± 0.08**	**222.19**	**<0.001**
Father plumage colour	**0.08 ± 0.12**	**0.45**	**0.500**
Moonlight	**0.03 ± 0.08**	**0.21**	**0.646**
Father plumage colour × Moonlight	0.05 ± 0.08	0.04	0.525
Moonlight × Rank	-0.02 ± 0.08	0.04	0.519
Father plumage colour × Rank	**-0.16 ± 0.08**	**3.77**	**0.052**
Father plumage colour × Moonlight × Rank	0.05 ± 0.08	0.34	0.561

* Estimates based on standardized variables and a logit link.

** Sex effects are given as male minus female estimates.



Supplementary Figure 3 | Nestling fledging success and brood size in the barn owl. A. Fledging success in relation to rank in the within-brood age hierarchy (hatching order). Low-rank (i.e. the first-hatched individuals) nestlings exhibit a high survival, whereas survival in high-rank nestlings decays rapidly below the 60% (horizontal red line). **B.** Distribution of brood sizes at hatching (*N* = 1,087 nests between 1996 and 2014) in the study population.

Supplementary Table 7 | Effect of moonlight and father plumage colouration on fledging success of nestlings born above rank 7. Results from a quasi-binomial generalized linear mixed model on fledging success of 217 barn owl nestlings from 150 broods. Model's marginal R^2 = 0.193, conditional R^2 = 0.981. Terms included in the final model are highlighted in bold.

Random effects

Parameter	**Variance**	**Lower 95% IC**	**Upper 95% IC**	**% Variance Explained**
Brood raised (*Intercept*)	8.56	8.37	8.76	54.87
Year (*Intercept*)	3.74	3.08	4.40	23.96

Fixed effects

Parameter	**Estimate* ± s.e.**	***t***	**d.f.**	***P***
Intercept	**-1.39 ± 1.13**	**-1.23**	**129**	**0.220**
Date	**1.29 ± 3.11**	**0.42**	**62**	**0.679**
Date^2	**-1.91 ± 3.08**	**-0.62**	**62**	**0.538**
Brood size	**1.23 ± 0.38**	**3.21**	**129**	**0.002**
Rank within brood hierarchy	**-1.33 ± 0.21**	**-6.25**	**62**	**<0.001**
Father plumage colour	**-0.54 ± 0.34**	**-1.60**	**129**	**0.112**
Moonlight	**0.42 ± 0.27**	**1.52**	**62**	**0.133**
Father plumage colour × Moonlight	**-0.79 ± 0.31**	**-2.58**	**62**	**0.012**

* Estimates based on standardized variables a logit link.

Supplementary Table 8 | Effect of moonlight, cloudiness and father plumage colouration on fledging success of nestlings born above rank 7 in the barn owl. Results from a quasi-binomial generalized linear mixed model on fledging success of 217 barn owl nestlings. The model was run considering the same random effects than in the model presented in the Supplementary Table 7. Terms included in the final model are highlighted in bold.

Parameter	***t***	**d.f.**	***P***
Intercept	**0.25**	**129**	**0.801**
Date	**0.24**	**61**	**0.811**
Date^2	**-0.49**	**61**	**0.624**
Brood size	**3.19**	**129**	**0.002**
Rank within brood hierarchy	**-7.02**	**61**	**0.000**
Father plumage colour	**-1.45**	**129**	**0.151**
Moonlight	**1.96**	**61**	**0.055**
Cloudiness	**-3.21**	**61**	**0.002**
Father plumage colour × Moonlight	**-2.88**	**61**	**0.006**

Supplementary Table 9 | Association between male plumage colouration and moonlight conditions the night the females laid their first egg (a), the night the first in-nest copulations are expected to occur (b), and the night nestling of rank 6 to 8 are expected to become 15 days old (c). Shown are the results from generalized linear mixed models on moonlight conditions as a binary response variable (≥ 50% of the Moon illuminated *vs.* < 50% of the Moon illuminated). Sample size of 1,293 clutches of 631 males from 1994 to 2017. Models' marginal $R^2 = 0.009$, $R^2 = 0.005$, and $R^2 = 0.007$, conditional $R^2 = 0.05$, $R^2 = 0.035$ and $R^2 = 0.04$.

a. Moonlight conditions the night the females laid their first egg

Random effects

Parameter	**χ^2 (d.f.)**	***P***	**Variance**	**% Variance Explained**
Male ID (*Intercept*)	1.54	0.215	0.108	3.11
Year (*Intercept*)	2.03	0.154	0.036	1.06

Fixed effects

Parameter	**Estimate* ± s.e.**	***z***	***P***
Intercept	0.15 ± 0.07	2.05	0.040
Male plumage colouration	-0.17 ± 0.06	-2.87	0.004

b. Moonlight conditions the night first in-nest copulations are expected to occur

Random effects

Parameter	**χ^2 (d.f.)**	***P***	**Variance**	**% Variance Explained**
Male ID (*Intercept*)	0.37	0.543	0.054	1.59
Year (*Intercept*)	1.87	0.107	0.047	1.39

Fixed effects

Parameter	**Estimate* ± s.e.**	***z***	***P***
Intercept	0.19 ± 0.07	2.52	0.012
Male plumage colouration	-0.13 ± 0.06	-2.28	0.023

c. Moonlight conditions the night nestling of rank 6 to 8 are expected to become 15 days old

Random effects

Parameter	**χ^2 (d.f.)**	***P***	**Variance**	**% Variance Explained**
Male ID (*Intercept*)	1.35	0.245	0.101	2.96
Year (*Intercept*)	0.06	0.808	0.006	0.18

Supplementary Table 9: *Continued*

Fixed effects

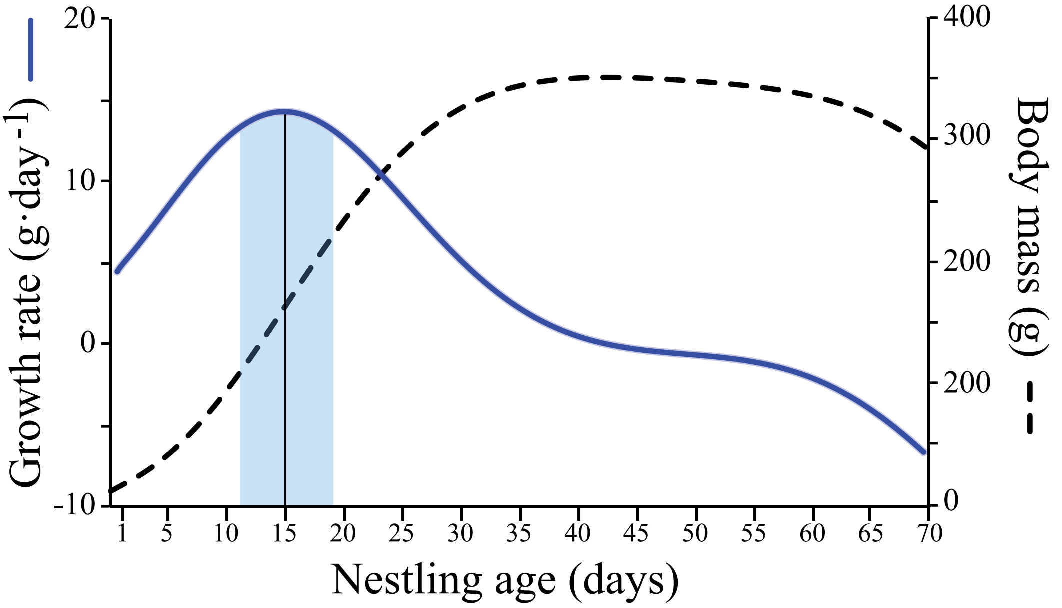
Parameter	**Estimate* ± s.e.**	***z***	***P***
Intercept	0.14 ± 0.06	2.27	0.023
Male plumage colouration	-0.15 ± 0.06	-2.61	0.009

Supplementary Table 10 | Statistical results when including spottiness as covariable into the statistical models. Shown are the results obtained from the same statistical models as presented along the supplementary tables 1-2, and 5-9, but including spottiness as covariable. Spottiness was calculated as product of the mean number of spots and the mean area occupied by the spots (calculated from mean spot diameter). The specific statistic used in each test can be found on the supplementary tables presenting the main results without including spottiness.

Parameter	**Statistic**	**d.f.**	***P***
A. Parental food provisioning			
Intercept	6.71	1	<0.001
Brood size	2.56	1	0.010
Sex**	8.17	1	<0.001
Brood size × Sex**	-1.52	1	0.128
Laying date	1.85	1	0.064
Laying date^2	-1.87	1	0.061
Spottiness	-1.21	1	0.227
Moonlight	-4.62	1	<0.001
Plumage colour	0.06	1	0.952
Moonlight × Plumage colour	-2.23	1	0.026
B. Male hunting success			
Intercept	-8.76	1	<0.001
Brood size	0.70	1	0.485
Laying date	-1.76	1	0.079
Laying date^2	1.77	1	0.077
Time of observation	-2.54	1	0.011
Time of observation^2	2.58	1	0.010
Time of observation^3	-2.63	1	0.008
Year	-1.07	1	0.286
Spottiness	-0.80	1	0.424
Hunting effort	-0.32	1	0.746
Plumage colour	0.55	1	0.585
Moonlight	-1.28	1	0.202
Plumage colour × Moonlight	-2.27	1	0.023
Plumage colour × Hunting effort	1.52	1	0.128
Moonlight × Hunting effort	0.44	1	0.657
Plumage colour × Moonlight × Hunting effort	-2.48	1	0.013
C. Nestling body mass			
Intercept	515770.0	1	<0.001
Sex**	190.9	1	<0.001
Laying date	49.2	1	<0.001
Age	51024.0	1	<0.001
Age^2	16414.0	1	<0.001
Age^3	6642.5	1	<0.001

Supplementary Table 10: *Continued*

Age^4	3284.8	1	<0.001
Brood Size	53.8	1	<0.001
Rank within brood hierarchy	508.3	1	<0.001
Hour	106.3	1	<0.001
Hour^2	87.9	1	<0.001
Hour^3	44.0	1	<0.001
Spottiness	0.2	1	0.646
Father plumage colour	3.0	1	0.084
Moonlight	0.4	1	0.508
Moonlight × Father plumage colour	4.3	1	0.038
D. Nestling survival (all ages)			
Intercept	89.27	1	<0.001
Sex**	0.31	1	0.574
Laying date	3.67	1	0.055
Laying date^2	5.65	1	0.017
Brood size	27.91	1	<0.001
Rank within brood hierarchy	220.27	1	<0.001
Spottiness	<0.01	1	0.958
Father plumage colour	0.06	1	0.807
Moonlight	0.24	1	0.622
Father plumage colour × Moonlight	0.27	1	0.604
Father plumage colour × Rank	2.93	1	0.087
E. Nestling survival (nestlings born above rank 7)			
Intercept	0.24	1	0.808
Date	0.62	1	0.535
Date^2	-0.83	1	0.408
Brood size	3.17	1	0.002
Rank within brood hierarchy	-6.04	1	<0.001
Spottiness	-1.48	1	0.141
Father plumage colour	-1.33	1	0.185
Moonlight	1.36	1	0.178
Father plumage colour × Moonlight	-2.83	1	0.006
F. Moonlight the night females laid their first egg			
Intercept	2.34	1	0.019
Spottiness	-0.52	1	0.600
Plumage colouration	-2.56	1	0.010
F. Moonlight the night first in-nest copulations are expected to occur			
Intercept	2.31	1	0.021
Spottiness	-0.17	1	0.865
Plumage colouration	-2.42	1	0.015
H. Moonlight conditions the night nestling of rank 6 to 8 are expected to become 15 days old			
Intercept	2.35	1	0.019
Spottiness	-0.63	1	0.525
Plumage colouration	-2.31	1	0.021



Supplementary Figure 4 | Growth rate and body mass gain in barn owl nestlings. Shown are estimated values (see Supplementary Table 5) of body mass and growth rate from the studied population. Maximal growth rate occurs at 15 days of age (black vertical line). Area depicted in light blue indicates the nestling age range considered to analyse the difference in parental food provisioning between owlets that fledged and those that did not fledge (see Results).

Supplementary Table 11 | Effect of moonlight and father plumage colouration on the number of uneaten common voles (*Microtus arvalis*) found in the nest-boxes. Shown are the results from a Poisson generalized linear-mixed model on the number of fresh common voles found still uneaten by the female or the owlets when monitoring the nests (*N* = 210 observations obtained in 116 nests over 15 years). For this analysis, prey cannot be directly attributed to one of the parents. However, given that the hunting effort is larger in males than in females, who may still be incubating or taking care of the chicks rather than hunting, we only considered male colouration. Age of the elder nestling was included to account for the level of development of the brood. Terms included in the final model are highlighted in bold.

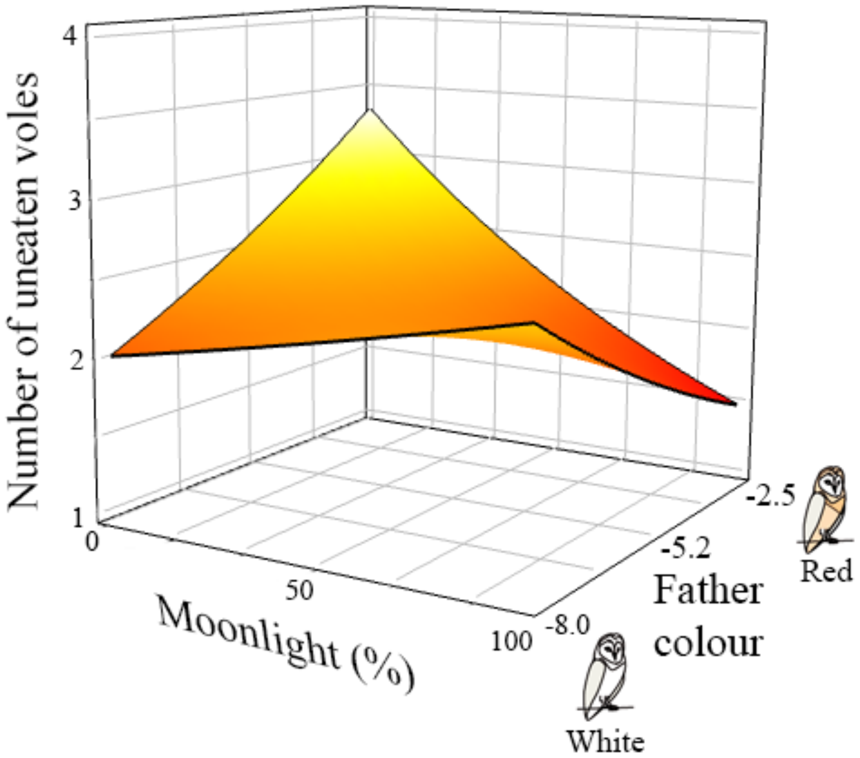
Random effects

Parameter	**Variance**	**% Variance Explained**
Parent ID (*Intercept*)	0.149	24.34
Site ID (*Intercept*)	0.028	0.046
Year (*Intercept*)	0.279	45.59

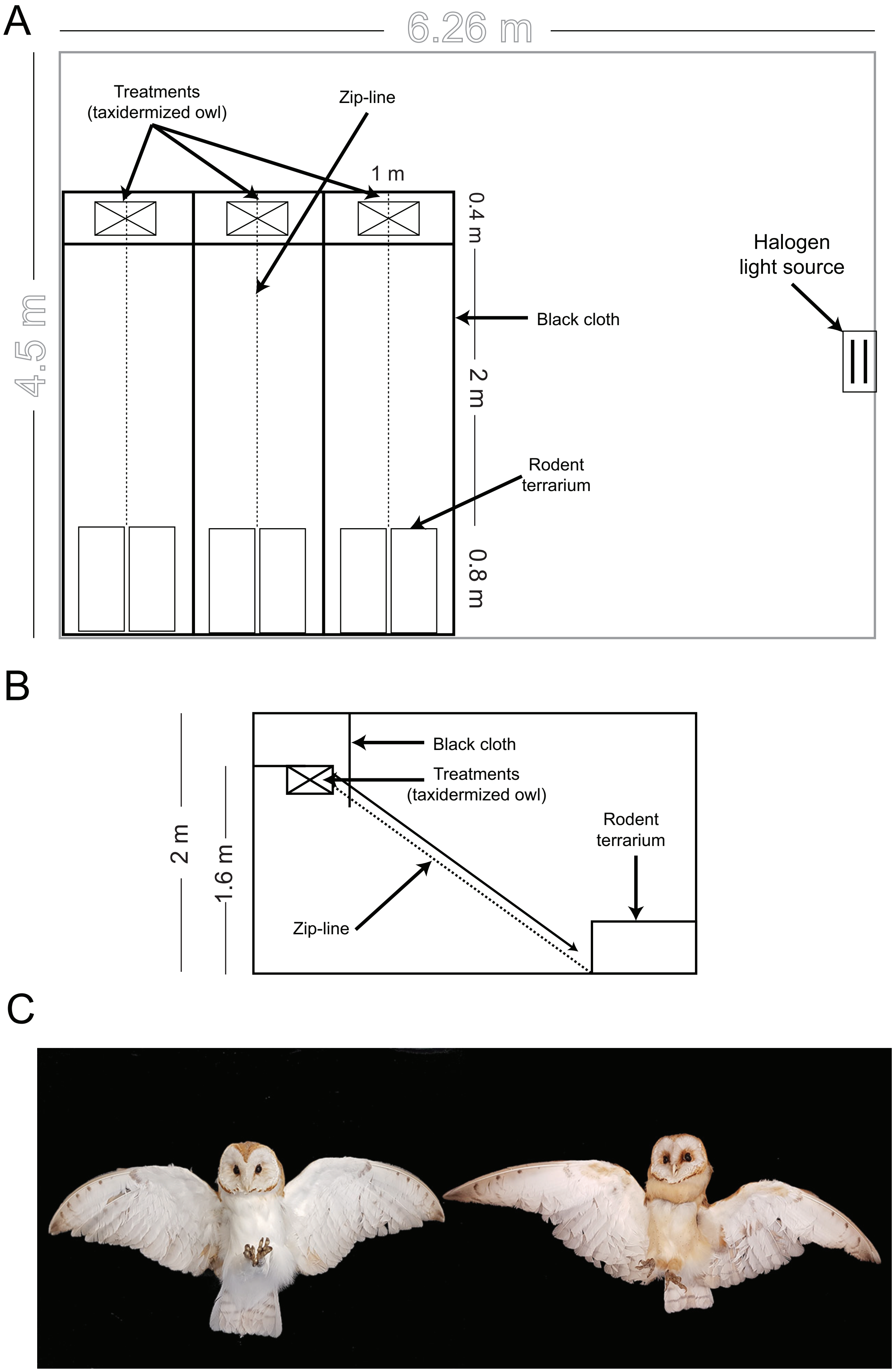
Fixed effects

Parameter	**Estimate* ± S.E.**	***z*-test**	***P***
Intercept	**0.82 ± 0.18**	**4.61**	**<0.001**
Brood size	**0.17 ± 0.06**	**2.82**	**0.005**
Age of the elder nestling	**-0.07 ± 0.07**	**1.08**	**0.279**
Sampling time	**0.02 ± 0.07**	**0.24**	**0.811**
Moonlight	**-0.02 ± 0.05**	**0.44**	**0.659**
Father plumage colour	**0.04 ± 0.07**	**0.65**	**0.518**
Moonlight × Father plumage colour	**-0.10 ± 0.05**	**2.11**	**0.035**

* Estimates based on standardized variables



Supplementary Figure 5 | Relationship between moonlight and father plumage colouration on the number of uneaten common voles (*Microtus arvalis*) found in the nest-boxes. Shown is the predicted surface from a Poisson-GLM model on the number of fresh common voles found still uneaten by the female or the owlets when monitoring the nests (N = 210 observations obtained in 116 nests over 15 years).


A
6.26 m
4.5 m
Treatments
(taxidermized owl)
Zip-line
1 m
0.4 m
Black cloth
2 m
Halogen
light source
Rodent
terrarium
0.8 m
B
Black cloth
Treatments
(taxidermized owl)
Rodent
terrarium
2 m
1.6 m
Zip-line
C

Supplementary Figure 6 | Description of the experimental room. A. Scaled above view of the experimental setup used to study the anti-predatory response of voles to dark reddish and white owls. **B.** Detailed lateral view of one of the lines, describing the zipline system use to mimic owl attacks on the voles. **C.** Pictures of one of the white (score -8) and one of the red (score -3.5) taxidermized owls used for the behavioural experiments.

Supplementary Table 12 | Model selection and description based on AIC values. Model ranking based on AICc values for the main parameters presented in the text (parental food provisioning, A, male hunting success, B, vole probability to detect an owl, C, time voles spent frozen, D, and nestling body mass, E, and survival, F). Analysis on the survival of nestlings above rank 7 (Supplementary Tables 8 and 9) was run using a quasi-likelihood approach and no AIC values could be derived. Models were conducted using the *MuMIn* package. Provided are the AICc values and the difference in AICc between each model and the best model (ΔAICc), model weight (*w*) and the evidence ratio for each model to the best model (ER). Models selected as best using backward elimination are highlighted in bold. Model parameters are indicated using R notation (i.e., an asterisk between two terms indicates that additive and interactive effects of these terms were included in the models whereas a colon makes reference only to the interaction between terms).

Rank	AICc	ΔAICc	*w*	ER	Model parameters
A. Parental food provisioning					
1	5189.4	**-**	**0.19**	**-**	**~ Sex*Brood size + Laying date + Laying date^2 + Moonlight*Plumage colour**
2	5189.6	0.55	0.15	1.31	~ Sex*Brood size + Laying date + Laying date^2 + Moonlight*Plumage colour + Moonlight:Sex
3	5189.7	0.70	0.14	1.42	~ Sex*Brood size + Laying date + Laying date^2 + Moonlight*Plumage colour + Plumage colour:Sex
4	5189.9	0.89	0.12	1.56	~ Sex*Brood size + Laying date + Laying date^2 + Moonlight*Plumage colour + Plumage colour:Sex + Moonlight:Sex
5	5191.0	1.95	0.07	2.65	~ Sex*Brood size + Laying date + Laying date^2 + Sex*Moonlight*Plumage
6	5191.6	2.56	0.54	3.60	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight*Plumage Colour
7	5192.0	2.97	0.04	4.41	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight*Plumage Colour + Plumage Colour:Sex
8	5192.1	3.06	0.04	4.62	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight*Plumage colour + Moonlight:Sex
9	5192.1	3.08	0.04	4.67	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight*Plumage colour + Plumage colour:Sex + Moonlight:Sex
10	5192.4	3.38	0.04	5.43	~ Sex*Brood size + Laying date + Laying date^2+ Moonlight + Plumage colour
11	5193.1	4.07	0.03	7.65	~ Sex + Brood size + Laying date + Laying date^2 + Sex*Moonlight*Plumage colour
12	5193.1	4.09	0.03	7.72	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight*Plumage colour + Plumage colour:Sex
13	5194.5	5.42	0.01	15.03	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight*Plumage colour + Moonlight:Sex

Supplementary Table 12: *Continued*

14	5194.5	5.47	0.01	15.42	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight + Plumage colour
15	5194.9	5.90	0.01	19.15	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight + Plumage colour + Plumage colour:Sex
16	5195.2	6.11	0.01	21.18	~ Sex * Brood size + Laying date + Laying date^2 + Moonlight + Plumage colour + Plumage colour:Sex + Moonlight:Sex
17	5196.5	7.50	0.00	42.43	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight + Plumage colour + Moonlight:Sex
18	5196.9	7.89	0.00	51.80	~ Sex + Brood size + Laying date + Laying date^2 + Moonlight + Plumage colour + Plumage colour:Sex + Moonlight:Sex
B. Male hunting success					
1	**18232.9**	**0.00**	**0.28**	**1.00**	**~ Brood size + Laying date + Laying date^2 + Time + Time^2 + Time^3 + Year + Hunting effort*Plumage colour*Moonlight**
2	18233.4	0.49	0.22	1.28	~ Brood size + Laying date + Laying date^2 + Time + Time^2 + Time^3 + Year + Hunting effort*Plumage colour+Moonlight
3	18234.5	1.60	0.13	2.23	~ Brood size + Laying date + Laying date^2 + Time + Time^2 + Time^3 + Year + Hunting effort + Plumage colour + Moonlight
4	18234.9	1.96	0.10	2.67	~ Brood size + Laying date + Laying date^2 + Time + Time^2 + Time^3 + Year + Hunting effort*Plumage colour + Moonlight*Plumage colour
5	18235.2	2.25	0.09	3.08	~ Brood size + Laying date + Laying date^2 + Time + Time^2 + Time^3 + Year + Hunting effort*Plumage colour + Hunting effort *Moonlight
6	18235.9	3.00	0.06	4.48	~ Brood size + Laying date + Laying date^2 + Time + Time^2 + Time^3 + Year + Hunting effort + Plumage colour*Moonlight
7	18236.4	3.48	0.05	5.70	~ Brood size + Laying date + Laying date^2 + Time + Time^2 + Time^3 + Year + Plumage colour + Hunting effort *Moonlight
8	18236.7	3.73	0.04	6.45	~ Brood size + Laying date + Laying date^2 + Time + Time^2 + Time^3 + Year + Hunting effort*Plumage colour + Hunting effort *Moonlight + Plumage colour* Moonlight
9	18237.8	4.88	0.02	11.47	~ Brood size + Laying date + Laying date^2 + Time + Time^2 + Time^3 + Year + Hunting effort *Moonlight + Plumage colour* Moonlight
C. Vole probability to detect an owl					
1	**489.54**	**-**	**0.31**	**1**	**~ Moonlight condition + Plumage colour + Year + Repetition**
2	490.57	1.03	0.18	1.67	~ Moonlight condition + Plumage colour * Year + Repetition
3	490.87	1.33	0.16	1.94	~ Moonlight condition * Plumage colour + Year + Repetition
4	491.65	2.11	0.11	2.87	~ Moonlight condition * Year + Plumage colour + Repetition
5	492.11	2.56	0.09	3.6	~ Moonlight condition * Plumage colour + Plumage colour * Year + Repetition
6	492.69	3.15	0.06	4.82	~ Moonlight condition * Year + Plumage colour * Year + Repetition
7	492.99	3.45	0.05	5.6	~ Moonlight condition * Year + Moonlight condition * Plumage colour + Repetition
8	494.23	4.69	0.03	10.43	~ Moonlight condition * Year + Moonlight condition * Plumage colour + Plumage colour * Year + Repetition
9	496.16	6.61	0.01	27.31	~ Moonlight condition * Year * Plumage colour + Repetition
D. Time voles spent frozen					
1	**37.74**	**-**	**0.38**	**1**	**~ Moonlight condition * Plumage colour + Year**
2	39.3	1.55	0.17	2.18	~ Moonlight condition + Plumage colour + Year
3	39.32	1.58	0.17	2.2	~ Moonlight condition * Plumage colour + Moonlight condition * Year
4	40.46	2.71	0.1	3.89	~ Moonlight condition * Plumage colour + Year * Plumage colour
5	41.26	3.51	0.06	5.8	~ Moonlight condition + Plumage colour + Moonlight condition * Year

***Supplementary Table 12:** Continued*

6	41.74	3.99	0.05	7.37	~ Moonlight condition + Plumage colour + Year * Plumage colour
7	42.13	4.39	0.04	8.99	~ Moonlight condition * Plumage Colour + Year * Plumage colour + Moonlight condition * Year
8	43.85	6.11	0.02	21.25	~ Moonlight condition + Plumage colour + Year * Plumage colour + Moonlight condition * Year
9	45.03	7.28	0.01	38.16	~ Moonlight condition * Plumage colour * Year

E. Offspring body mass

1	**-28762**	**0**	**0.78**	**1**	**~Sex + Date + Age + Age^2 + Age^3 + ^{4} + Brood size + Rank + Date + Hour + Hour^2 + Hour^3 + Plumage colour * Moonlight**
2	-28759	2.51	0.22	3.51	~Sex + Date + Age + Age^2 + Age^3 + ^{4} + Brood size + Rank + Date + Hour + Hour^2 + Hour^3 + Plumage colour + Moonlight

F. Offspring survival

1	2385.98	1.62	0.17	2.24	**~Sex + Date + Date^2+ Brood size + Moonlight + Plumage colour * Rank**
2	2386.33	1.97	0.14	2.67	~Sex + Date + Date^2+ Brood size + Moonlight * Plumage colour + Plumage colour * Rank
3	2386.86	2.49	0.11	3.48	~Sex + Date + Date^2+ Brood size + Moonlight * Rank + Plumage colour * Rank
4	2387.93	3.57	0.06	5.96	~Sex + Date + Date^2+ Brood size + Moonlight + Plumage colour + Rank
5	2388.63	4.26	0.05	8.43	~Sex + Date + Date^2+ Brood size + Moonlight * Plumage colour + Rank* Plumage colour + Moonlight:Rank
6	2388.82	4.45	0.04	9.27	~Sex + Date + Date^2+ Brood size + Moonlight * Plumage colour + Rank
7	2389.61	5.25	0.03	13.78	~Sex + Date + Date^2+ Brood size + Moonlight * Rank + Plumage colour
8	2390.58	6.22	0.02	22.41	~Sex + Date + Date^2+ Brood size + Moonlight * Plumage colour * Rank
9	2384.36	0.00	0.38	1.00	~Sex + Date + Date^2+ Brood size + Moonlight * Plumage colour + Moonlight * Rank

Chapter 4

Moonlight drives foraging ground selection and prey capture in white barn owls *Tyto alba*

Robin Séchaud[1*], Kim Schalcher[1], Luis San-José Garcia[2], Nicolas Moulin[1], Bettina Almasi[3] and Alexandre Roulin[1]

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

[2] Laboratoire Évolution and Diversité Biologique, UMR 5174, CNRS, Université Toulouse III Paul Sabatier, Toulouse, France,

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

Chapter Status:

In preparation. The analyses presented in this chapter will be complemented with additional ones based on accelerometer data collected during the same period.

Author contributions:

All authors designed the project, A.R. et B.A. funded it. R.S., K.S. and N.M. collected the data. R.S., K.S., N.M. and L.M.S.-J. analysed the data. R.S. wrote the manuscript, with significant contributions of all authors.

Abstract

Variation in light levels is an important selective mechanism involved in the evolution and maintenance of colour polymorphism in animals. Although moonlight has been shown to alter the activity patterns of animals, its effects on nocturnal life, and in particular on the coloration of nocturnal animals, have so far received little attention. The barn owl *Tyto alba* is a nocturnal raptor that displays a ventral colour polymorphism, with plumage ranging from white to dark reddish-brown. Here, we further explore the interaction between moon illumination and colouration at night by studying how barn owls' foraging strategy (i.e. hunting on the wing or sit-and-wait), hunting ground selection and prey species caught vary with nocturnal light conditions. To do so, we GPS-tracked 132 male barn owls during the breeding period and installed camera traps in front of their nest to record the captured prey species. We showed that white owls foraged more in open landscape in moonlit conditions than in dark ones, whereas reddish owls did not select different foraging grounds depending on moon illumination. In addition, white owls captured more common voles *Microtus arvalis* in moonlit conditions than in dark ones, although we are unable to specify whether this is a result of the change in foraging ground selection or a capture advantage related to plumage colouration. In conclusion, our study provides empirical evidence that colouration plays an important role in nocturnal life, and that moon illumination might play a role in the evolution and maintenance of colour polymorphism of nocturnal animals.

Key words

Apodemus sp., Colour polymorphism, disruptive selection, light-heterogeneity, *Microtus arvalis*.

Introduction

Colour polymorphism has been described in many animal (Hoffman & Blouin, 2000; Roulin & Wink, 2004) and plant taxa (Armbruster, 2002; Brown & Clegg, 1984). As colouration plays multiple functions, from camouflage to sexual ornamentation, morphs can differ in background matching (Majerus, Brunton, & Stalker, 2000; Tsurui, Honma, & Nishida, 2010), habitat selection (Ahnesjö & Forsman, 2006; Muri et al., 2015), foraging success (Greco & Kevan, 1999; Tso, Tai, Ku, Kuo, & Yang, 2002), hunting strategy (Rohwer, 1990) or thermoregulation (Clusella Trullas, van Wyk, & Spotila, 2007; Hetem et al., 2009). Several hypotheses have been formulated to explain the evolution and maintenance of colour polymorphism (reviewed in Galeotti et al. 2003; Roulin 2004), among which disruptive selection has received the most support. It postulates that selective pressure might favour extreme morphs over intermediate ones under different environmental conditions (Mather, 1955; Rueffler, Van Dooren, Leimar, & Abrams, 2006). Even though the disruptive selective pressures are many and varied, environmental heterogeneity is a prerequisite for disruptive selection to occur, with different morphs exploiting different ecological niches (Skulason & Smith, 1995).

In birds, colour polymorphism is present in 61% of the orders and has evolved independently in different taxa (Galeotti et al., 2003). Most polymorphic bird species are predators (carnivorous, insectivorous or piscivorous) and live in heterogeneous habitats. This suggests that morphs may differ in conspicuousness to prey, predators or conspecifics depending on the environmental conditions. The conspicuousness of an animal’s colour pattern depends on how it matches with its background, which has been shown to vary with luminosity (Endler & Théry, 1996; Rohwer, 1990; San-Jose et al., 2019; Tate, Bishop, & Amar, 2016). Several recent studies have illustrated the complex interconnection between colouration and ambient light, such as, for example, the variation in bird coloration depending on exposure to light in rainforests (Gomez & Théry, 2004), or the spatial distribution of raptor colour morphs according to light variability (Passarotto, Parejo, Penteriani, & Avilés, 2018; Tate et al., 2016). Consequently, variation in light levels has been suggested to be an important selective mechanism involved in the evolution and maintenance of colour polymorphism in birds (Galeotti et al., 2003; McNaught & Owens, 2002).

Although moonlight has been shown to alter the activity patterns of animals (Clarke, Chopko, & Mackessy, 1996; Kotier, Brown, Mukherjee, Berger-Tal, & Bouskila, 2010; Pajot, Corbeau, Jambon, & Weimerskirch, 2021), it has rarely been considered as a potential driver of colour polymorphism evolution in nocturnal animals. Interestingly, Strigiformes, a group of mostly nocturnal birds (owls and nightjars), are the bird order with the greatest number of colour polymorphic species (33.5%; Galeotti et al., 2003), and polymorphic owls have been shown to be more present in habitats with variable light conditions (Passarotto et al., 2018). While colouration of nocturnal species has most often been claimed to be an adaptation to diurnal camouflage rather than to night time activity (Merilaita & Tullberg, 2005), it is now hypothesized that the colouration of nocturnal animals might be related to moon illumination (Galeotti et al., 2003; Passarotto et al., 2018).

The barn owl *Tyto alba* is a nocturnal raptor species that displays a genetically determined melanin-based colour polymorphism (Roulin, 2003). Its ventral plumage colouration ranges from white to dark reddish-brown, and has been linked to predator-prey interactions and nest site selection (Charter, Leshem, Meyrom, Peleg, & Roulin, 2012; Dreiss et al., 2012; Roulin, 2004a). Recently, San-Jose et al. (2019) showed that moonlight acts as disruptive agent in this species, with differently coloured owls varying foraging and breeding success depending on moon illumination. In moonlit nights, reddish owls had lower success in hunting and food provisioning than white ones, because the latter triggered longer freezing times in prey in this moon condition, facilitating their capture. Thus, the authors hypothesised that the white plumage displayed by some barn owls might provide a selective advantage in moonlit nights by exploiting the known aversion of rodents to bright light, making them easier to catch.

Here, we further explore this hypothesis by studying how barn owls adapt their behaviour and foraging strategies in relation to moon illumination. We GPS-tracked 132 male barn owls living in a semi-open landscape – with light-heterogeneity in the landscape created by forested areas providing shade in moonlit nights – and recorded their selection of perching locations and hunting grounds under varying ambient light conditions, as well as the time invested in each of the foraging techniques. Based on the previous study of San-Jose et al. (2019), we expect that during full-moon nights white owls should use open areas to benefit from the freezing effect their plumage has on rodents in order to increase hunting efficiency, while reddish owls might use the shaded areas provided by forests to benefit from a better camouflage. Accordingly, we expect white owls to hunt more on the wing to surprise its prey, while reddish ones might use more the sit-and-wait technique benefiting from its cryptic plumage. In addition, because light variation might also affect prey behaviour and ability to visually detect predators, we recorded the prey species captured by owls in different moonlight conditions using camera traps. As we predicted a change in forested habitat use in moonlit nights, we expect also in these conditions that white owls might capture more prey species exploiting open habitats (i.e. *Microtus sp.*), whereas reddish owls might prey more on woodland species (i.e. *Apodemus sp.*).

Materials and Methods

Study area

From 2016 to 2018, we monitored a wild population of barn owls breeding in nest boxes installed in barns in a typical Swiss farmland landscape. The study area is mainly composed of intensively exploited crops, interspersed with villages and forested areas (Frey, Sonnay, Dreiss, & Roulin, 2010; Séchaud et al., 2021). The latter is the main structural element in this homogeneous agricultural landscape, providing shelter against harsh weather conditions, but also producing light-heterogeneity during moonlit nights by creating shaded areas.

Colour measurement

We scored barn owl's colouration on the breast, belly, flank and underside of the wings using an eight colour chip ranging from 1 for reddish-brown to 8 for white (Roulin, Richner, & Ducrest, 1998), a method validated by comparison with spectrophotometric measurements (Dreiss & Roulin, 2010). In the following analyses, we used two different plumage colour classifications. First, we averaged the colour of all body parts to get a continuous colour parameter and, second, we classified the owls into three distinct colour morphs depending on their ventral (breast and belly) plumage colouration. The first two morphs are uniformly coloured, either entirely white or reddish, and the third one characterizes "intermediate" birds that are reddish on the breast and white on the belly (Fig S1). Analyses performed using the continuous colouration and classification in morphs presented similar results, we thus reported here only the ones including the continuous colouration to be comparable with previous studies (Table S1; San-Jose et al., 2019).

GPS tag deployment

Male adult barn owls were captured in their nest box (authorizations of the Department of the consumer and veterinary affairs: VD 2844 and 3213), approximately 3 weeks after the first nestling hatched. We attached GiPSy-5 GPS tags (Technosmart, Italy) on their back with a Teflon harness. Including the battery, the tags measured 30x20x10 mm and weighed approximately 12 grams, and were coupled with a 40mm long antenna. They were programmed to collect location and time every 10 seconds at night, from 30 minutes before dusk until 30 minutes after dawn to ensure the recording of their entire nocturnal activity. Two weeks later, the owls were recaptured and the tags recovered. The GPS data is stored in Movebank (www.movebank.org) and accessible under the project named "Barn owl (*Tyto alba*)" (Movebank ID 231741797). We obtained usable data for 132 male barn owls and, prior to any analysis, GPS data were pre-processed and filtered for aberrant positions using speed (excluding locations with a speed higher than 15 m/s) and location (excluding locations outside the study area). From the 1’012’981 positions recorded, 1’022 were removed and 1’011’959 were kept for the following analyses, all conducted with R v3.5.1 (R Core Team, 2018).

Behaviour annotation

To distinguish behavioural modes in the barn owl GPS tracks, we used the Expectation-Maximization binary Clustering method (EMbC), an unsupervised algorithm that clusters movement data based on speed and turning angle between locations (Garriga, Palmer, Oltra, & Bartumeus, 2016). The three behavioural modes detected were perching, hunting and commuting, and represent the three main movement behaviours displayed by barn owls outside of their nests (detailed in Séchaud et al., 2021).

Rather than considering each location point independently, they were grouped into behavioural events. Commuting tracks were excluded from the analyses to keep only perching and hunting behavioural modes as they reflect alternative foraging strategies. For each perching and hunting event, we extracted the distance to the closest forested areas. The positioning of the forests in the landscape were obtained from the Swiss TLM3D catalogue (Swiss Topographic Landscape Model).

Prey species identification

When a breeding male barn owl was equipped with GPS devices, we installed a camera trap (HC500 HyperFire, Reconyx) at the entrance of the nest box to record its feeding events. Adult barn owls bring a single prey item per nest visit and the male is the main contributor to the feeding of the nestlings (Roulin, Ducrest, & Dijkstra, 1999). For each feeding event pictured by the camera trap, we determined the prey captured at the genus level. When the bird identity could not be clearly recognised on the camera trap picture, we used the GPS location of the owls to confirm the identity of the feeder. We obtained reliable data (sufficient number of prey identified and wide enough recording period) for 77 broods, corresponding to a total of 3’364 prey captured by males identified (44 prey item on average per male; range: 18 to 117).

Moon illumination

We extracted the percentage of the moon illuminated (moon fraction), altitude and presence – when above the horizon – depending on the owl’s location using the *suncalc* R package (Thieurmel & Elmarhraoui, 2019). From the same tool, we extracted dawn and dusk times and calculated the time after dawn for each hunting or perching event. Barn owls being strictly active at night in the study area, no GPS tracks were recorded after dawn or before dusk. Because cloudiness is likely to mitigate the effect of moonlight, we obtained Total Cloud Cover (TCC) data from the “ERA5 hourly data on single levels from 1979 to present" dataset from the Copernicus platform (Hersbach et al., 2018), at a temporal resolution of 1h and spatial resolution of 0.25 x 0.25 degrees grid.

We estimated moon illumination with three different formulas used in recent literature. First, we calculated the moon illumination as the percentage of the moon illuminated, while setting its value to 0 if the moon was below the horizon (San-Jose et al., 2019). Second, the moon altitude above the horizon was included in the calculation (Kyba, Conrad, & Shatwell, 2020; Pajot et al., 2021). Third, in addition to the moon altitude, the cloudiness and its mitigating effect on illumination was taken into account by including the TCC in the formula (Pajot et al., 2021). The illumination data obtained with these three formulas were compared to the night luminance measured on the ground at a meteorological station in the center of the study area (Table S2). The squared-value of the moon illumination data obtained with the second formula – taking into account moon presence, illuminated fraction and elevation – fitted the most the luminance measured on the ground and was thus used in the following statistical analyses (Figure S1).

Statistical analyses

Foraging strategy

We extracted the time spent hunting or perching per night for each owl, and modelled the foraging strategy used per night by comparing the time invested hunting on the wing or perched using generalised linear mixed-effect models with a binomial distribution, using the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). Fixed effects included moon illumination, plumage colouration and their interaction, as well as year, date, duration of the night (time between dawn and dusk) and the number of nestlings. We found no quadratic and cubic effects of the date, and thus did not include it in the final model. The individual ID was included as random factors. Preliminary analyses showed that neither the male's body mass, nor its size (i.e. wing length, a good proxy for size in birds) had an effect in this and all subsequent analyses, and thus we did not include them in the final models to simplify them.

Foraging ground selection

We modelled the effect of moon illumination and plumage colouration on the distance to the closest forested areas (square root transformed) using linear mixed-effect models (Bates et al., 2015). We ran one model for each behavioural mode. Fixed effects included moon illumination, plumage colouration and their interaction, as well as year, date (linear, quadratic and cubic), hours after dawn (linear and quadratic) and the number of nestlings. The night ID and the individual ID were included as random factors.

Prey species captured

The common vole *Microtus arvalis* and mice *Apodemus sp.* species (wood mouse *Apodemus sylvaticus* and yellow-necked mouse *Apodemus flavicollis*) are the main prey eaten by barn owls in Switzerland (Frey et al., 2010; Roulin, 2004a), the former being commonly found in open areas and the latter being related to woodland. To measure an alteration in diet associated with a change in forested areas use, we modelled the effect of moon illumination and plumage colouration on the probability of capturing *Microtus* and *Apodemus* species by building two generalised linear mixed-effect models with a binomial distribution. We used the same fixed and random variables as in the habitat selection model above, with the exception that we removed the quadratic and cubic terms for date and hours after dawn parameters as they were not significant.

Results

Foraging strategy

Neither the moon illumination, nor the plumage colouration, nor their interaction were significantly related to the owl's foraging strategy (i.e. hunting on the wing or sit-and wait; Table 1). The foraging strategy used was influenced by the date (Figure 1), with owls hunting more on the wing in the beginning of the breeding season than at the end, and the year. The proportion of time spent hunting on the wing showed a tendency, although not significant, to decrease with the duration of the night, but was not related to the number of nestlings (Table 1).

Foraging ground selection

The interaction between moon illumination and plumage colouration had a significant effect on the distance to the forest of owls when hunting on the wing, but not when perched (Table 2). Pale males hunted on the wing further from the forest in moonlit nights, while red males did not adapt their behaviour according to moonlight (Figure 2). Moon illumination and plumage colouration were both positively related to the forest distance for both foraging techniques (Figures 3a and b). Owls foraged closer to forests in 2017 than in the two other years. The date had a quadratic relationship with the distance to the forest, with males being closer to the forest at the beginning of the season (Figure 3c). The number of hours after dawn also had a significant quadratic relationship with the distance to the forest, with owls being closer to forest in the middle of the night than near dawn and dusk (Figure 3d). Finally, the number of nestlings was positively correlated to the distance to the forest (Table 2).

Prey species captured

Among the 3’364 prey captured by male barn owls, the vast majority of which were common voles (*Microtus sp*.; 73.3%), followed by mice (*Apodemus sp*.; 16.2%), water voles (*Arvicola terrestris*; 8.4%) and shrews (*Corcidura/Sorex sp*.; 1.6%). The last 0.5% was comprised of other mammal (6 hazel dormouse *Muscardinus avellanarius*, 2 common moles *Talpa europaea* and 1 edible dormouse *Glis glis*) and bird species (7 house sparrow *Passer domesticus*, 1 common redstart *Phoenicurus phoenicurus* and 1 eurasian skylark *Alauda arvensis*).

The interaction between moon illumination and plumage colouration significantly affected the proportion of *Microtus sp.* captured by differently coloured owls (Table 3), with red owls catching more of them during moonless nights than white owls (Figure 4). White owls preyed more frequently on *Apodemus* sp. than red owls (Figure 5a), independently of moon illumination, while a nearly-significant opposite tendency was observed for Microtus arvalis (Figure 5b). The proportion of prey species consumed also varied between years and with date (Figures 5c and d), but not within the night, nor with the number of nestlings (Table 3).

Discussion

In this study, we showed that moon illumination impacts differently pale and red barn owls in their hunting ground selection and prey species capture, suggesting that moonlight plays a role in the evolution and maintenance of colour polymorphism of nocturnal animals. More generally, our results highlighted that barn owls with different plumage coloration use different resources, supporting the hypothesis that the colour variation observed in this species is probably maintained by disruptive selection.

White owls foraged more in open landscape in moonlit conditions than in dark ones, whereas reddish owls did not select different foraging grounds depending on moon illumination. Indeed, reddish owls foraged closer to the forest than white ones, regardless of moon illumination. This result is consistent with the background matching hypothesis (Endler, 1981; Merilaita, Scott-Samuel, & Cuthill, 2017), with reddish owls being more cryptic in dark habitats – close to forested areas – independently of illumination conditions, whereas paler ones might be less conspicuous on a clear and moonlit sky. Such pattern has already been described in herons and diurnal raptor species (Rohwer, 1990; Tate et al., 2016), in which white and dark colour morphs benefit from hunting against bright and dark skies, respectively. This behavioural adaptation of white barn owls to moon illumination may allow them to maintain constant food provisioning and hunting success as seen in a previous study, whereas red ones do not (San-Jose et al., 2019).

We found that white owls captured more common voles in moonlit conditions than in dark ones, although we are unable to specify whether this is a cause of the change in foraging ground selection or a capture advantage related to plumage colouration. Interestingly, San-Jose et al. (2019) showed that the white plumage displayed by barn owls induced longer freezing times in their main prey, the common vole *Microtus arvalis*, which might consequently facilitate their capture. But, and contrary to our predictions, we did not detect any change in the owl's foraging strategy – hunting on the wing or perched – in relation to moon illumination. The hunting advantage associated to white plumage may thus not be used deliberately by white owls, but rather a by-product of hunting in open areas during moon illuminated nights. However, it is worth nothing that we considered foraging behaviour at the night level and we thus cannot exclude that owls adapted their strategies at a finer scale. For example, as eagle owls *Bubo bubo* take advantage of moon luminosity to render their white throat patches more visible to conspecifics (Penteriani et al., 2007; Penteriani, Delgado, Campioni, & Lourenço, 2010), white barn owls could orient themselves in relation to the moon to make their plumage more brilliant and exploit rodent's known aversion to light (Bourin, Petit-Demoulière, Nic Dhonnchadha, & Hascöet, 2007; Lockard, 1963).

Here, we showed that owls with different plumage colouration differ in their foraging ground selection and prey species captured, providing support to previous studies which suggested that the colour polymorphism observed in this species could be maintained by disruptive selection (Roulin, 2004b, 2004a; Roulin & Wink, 2004; San-Jose et al., 2019). Surprisingly, although white owls foraged further away from forests than red ones, they also captured more *Apodemus* sp., which are normally forest-dwelling species. We hypothesize that these mice species might display different escape responses when attacked by white or red barn owls, as it has already been shown in the common vole (San-Jose et al., 2019). This should be measured under controlled conditions, accounting also for the foraging strategy used, hunting on the wing or perched. In addition, barn owl colouration follows a clinal distribution in Europe, which varies from white in Iberia to dark rufous in North-eastern Europe, maintained by selective pressures still to be identified (Antoniazza et al., 2014; Burri et al., 2016). Roulin (2004a) showed that, in Europe, the proportion of *Apodemus* and *Microtus* species in the barn owl diet respectively decreases and increases with latitude, and our results indicate a similar colour-specific diet pattern in Switzerland. This suggests that the colour cline observed in European barn owls might be maintained by colour-specific predator-prey interactions.

In conclusion, our study showed that moon illumination induces different foraging ground selection and prey species capture in relation to barn owl plumage colouration. These results, combined with the recent studies on colour vision in nocturnal species (see Kelber & Roth, 2006), provide evidence that colouration plays an important role in nocturnal life. Additionally, night illumination variations induced by the moon phase and elevation might play a role in the evolution and maintenance of colour polymorphism of nocturnal animals, as it seems to be the case in the barn owl. Habitat structure and predator-prey interactions are probably the two main disruptive forces maintaining colour variation in this species, and future studies should experimentally investigate the interaction between the two.

Acknowledgements

We thank Carolina Massa, Charlène Gémard, Estelle Mayor, Steve Zurkinden, Céline Plancherel, Raphaël Sartori, Christophe Sahli, Marie Déturche, Maxime Chèvre, Jonathan Ehinger and Nadine Apolloni for help with collecting field data. This study was financially supported by the Swiss National Science Foundation (grants no. 31003A_173178).

References

Ahnesjö, J., & Forsman, A. (2006). Differential habitat selection by pygmy grasshopper color morphs; interactive effects of temperature and predator avoidance. *Evolutionary Ecology*, *20*(3), 235–257. doi:10.1007/s10682-006-6178-8

Antoniazza, S., Kanitz, R., Neuenschwander, S., Burri, R., Gaigher, A., Roulin, A., & Goudet, J. (2014). Natural selection in a postglacial range expansion: the case of the colour cline in the European barn owl. *Molecular Ecology*, *23*, 5508–5523. doi:10.1111/mec.12957

Armbruster, W. S. (2002). Can indirect selection and genetic context contribute to trait diversification? A transition-probability study of blossom-colour evolution in two genera. *Journal of Evolutionary Biology*, *15*(3), 468–486. doi:10.1046/j.1420-9101.2002.00399.x

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi:10.18637/jss.v067.i01

Bourin, M., Petit-Demoulière, B., Nic Dhonnchadha, B., & Hascöet, M. (2007). Animal models of anxiety in mice. *Fundamental and Clinical Pharmacology*, *21*(6), 567–574. doi:10.1111/j.1472-8206.2007.00526.x

Brown, B. A., & Clegg, M. T. (1984). Influence of Flower Color Polymorphism on Genetic Transmission in a Natural Population of the Common Morning Glory, *Ipomoea purpurea*. *Evolution*, *38*(4), 796–803.

Burri, R., Antoniazza, S., Gaigher, A., Ducrest, A. L., Simon, C., Fumagalli, L., … Roulin, A. (2016). The genetic basis of color-related local adaptation in a ring-like colonization around the Mediterranean. *Evolution*, *70*(1), 140–153. doi:10.1111/evo.12824

Charter, M., Leshem, Y., Meyrom, K., Peleg, O., & Roulin, A. (2012). The importance of micro-habitat in the breeding of Barn Owls *Tyto alba*. *Bird Study*, *59*(3), 368–371. doi:10.1080/00063657.2012.669360

Clarke, J. A., Chopko, J. T., & Mackessy, S. P. (1996). The effect of moonlight on activity patterns of adult and juvenile prairie rattlesnakes (*Crotalus viridis viridis*). *Journal of Herpetology*, *30*(2), 192–197. doi:10.2307/1565509

Clusella Trullas, S., van Wyk, J. H., & Spotila, J. R. (2007). Thermal melanism in ectotherms. *Journal of Thermal Biology*, *32*(5), 235–245. doi:10.1016/j.jtherbio.2007.01.013

Dreiss, A., Antoniazza, S., Burri, R., Fumagalli, L., Sonnay, C., Frey, C., … Roulin, A. (2012). Local adaptation and matching habitat choice in female barn owls with respect to melanic coloration. *Journal of Evolutionary Biology*, *25*(1), 103–114. doi:10.1111/j.1420-9101.2011.02407.x

Dreiss, A., & 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*(3), 689–704. doi:10.1111/j.1095-8312.2010.01503.x

Endler, J. A. (1981). An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society*, *16*(1), 25–31. doi:10.1111/j.1095-8312.1981.tb01840.x

Endler, J. A., & Théry, M. (1996). Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *American Naturalist*, *148*(3), 421–452. doi:10.1086/285934

Frey, C., Sonnay, C., Dreiss, A., & Roulin, A. (2010). Habitat, breeding performance, diet and individual age in Swiss Barn Owls (*Tyto alba*). *Journal of Ornithology*, *152*(2), 279–290. doi:10.1007/s10336-010-0579-8

Galeotti, P., Rubolini, D., Dunn, P. O., & Fasola, M. (2003). Colour polymorphism in birds: causes and functions. *Journal of Evolutionary Biology*, *16*(4), 635–646. doi:10.1046/j.1420-9101.2003.00569.x

Garriga, J., Palmer, J. R. B., Oltra, A., & Bartumeus, F. (2016). Expectation-Maximization Binary Clustering for Behavioural Annotation. *PLOS ONE*, *11*(3), e0151984. doi:10.1371/journal.pone.0151984

Gomez, D., & Théry, M. (2004). Influence of ambient light on the evolution of colour signals: Comparative analysis of a Neotropical rainforest bird community. *Ecology Letters*, *7*(4), 279–284. doi:10.1111/j.1461-0248.2004.00584.x

Greco, C. F., & Kevan, P. G. (1999). Polyethism in foraging in a polymorphic predator, *Enoplognatha ovata* (Araneae: Theridhdae): A case for balance. *Canadian Entomologist*, *131*(2), 259–268. doi:10.4039/ent131259-2

Hersbach, H., Bell, B., Berrisford, P., Biavati, G., Horányi, A., Muñoz Sabater, J., … Thépaut, J.-N. (2018). ERA5 monthly averaged data on single levels from 1979 to present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). doi:10.24381/cds.adbb2d47

Hetem, R. S., de Witt, B. A., Fick, L. G., Fuller, A., Kerley, G. I. H., Meyer, L. C. R., … Maloney, S. K. (2009). Body temperature, thermoregulatory behaviour and pelt characteristics of three colour morphs of springbok (*Antidorcas marsupialis*). *Comparative Biochemistry and Physiology, Part A*, *152*(3), 379–388. doi:10.1016/j.cbpa.2008.11.011

Hoffman, E. A., & Blouin, M. S. (2000). A review of colour and pattern polymorphisms in anurans. *Biological Journal of the Linnean Society*, *70*(4), 633–665. doi:10.1006/bijl.1999.0421

Kelber, A., & Roth, L. S. V. (2006). Nocturnal colour vision - not as rare as we might think. *Journal of Experimental Biology*, *209*, 781–788. doi:10.1242/jeb.00571

Kotier, B. P., Brown, J., Mukherjee, S., Berger-Tal, O., & Bouskila, A. (2010). Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. In *Proceedings of the Royal Society B: Biological Sciences* (Vol. 277, pp. 1469–1474). Royal Society. doi:10.1098/rspb.2009.2036

Kyba, C. C. M., Conrad, J., & Shatwell, T. (2020). Lunar illuminated fraction is a poor proxy for moonlight exposure. *Nature Ecology and Evolution*, *4*(3), 318–319. doi:10.1038/s41559-020-1096-7

Lockard, R. B. (1963). Some effects of light upon the behavior of rodents. *Psychological Bulletin*, *60*(6), 509–529. doi:10.1037/h0046113

Majerus, M. E. N., Brunton, C. F. A., & Stalker, J. (2000). A bird's eye view of the peppered moth. *Journal of Evolutionary Biology*, *13*(2), 155–159. doi:10.1046/j.1420-9101.2000.00170.x

Mather, K. (1955). Polymorphism as an Outcome of Disruptive Selection. *Evolution*, *9*(1), 52. doi:10.2307/2405357

McNaught, M. K., & Owens, I. P. F. (2002). Interspecific variation in plumage colour among birds: Species recognition or light environment? *Journal of Evolutionary Biology*, *15*(4), 505–514. doi:10.1046/j.1420-9101.2002.00431.x

Merilaita, S., Scott-Samuel, N. E., & Cuthill, I. C. (2017). How camouflage works. *Philosophical Transactions of the Royal Society B: Biological Sciences*. Royal Society. doi:10.1098/rstb.2016.0341

Merilaita, S., & Tullberg, B. S. (2005). Constrained camouflage facilitates the evolution of conspicuous warning coloration. *Evolution*, *59*(1), 38–45. doi:10.1554/04-410

Muri, D., Schuerch, J., Trim, N., Golay, J., Baillifard, A., El Taher, A., & Dubey, S. (2015). Thermoregulation and microhabitat choice in the polymorphic asp viper (*Vipera aspis*). *Journal of Thermal Biology*, *53*, 107–112. doi:10.1016/j.jtherbio.2015.06.009

Pajot, A., Corbeau, A., Jambon, A., & Weimerskirch, H. (2021). Diel at-sea activity of two species of great albatrosses: the ontogeny of foraging and movement behaviour. *Journal of Avian Biology*, *52*(2). doi:10.1111/jav.02597

Passarotto, A., Parejo, D., Penteriani, V., & Avilés, J. M. (2018). Colour polymorphism in owls is linked to light variability. *Oecologia*, 1–13. doi:10.1007/s00442-018-4128-0

Penteriani, V., Delgado, M. del M., Alonso-Álvarez, C., Pina, N. V., Sergio, F., Bartolommei, P., & Thompson, L. J. (2007). The Importance of Visual Cues for Nocturnal Species: Eagle Owl Fledglings Signal with White Mouth Feathers. *Ethology*, *113*(10), 934–943. doi:10.1111/j.1439-0310.2007.01414.x

Penteriani, V., Delgado, M. del M., Campioni, L., & Lourenço, R. (2010). Moonlight Makes Owls More Chatty. *PLoS ONE*, *5*(1), e8696. doi:10.1371/journal.pone.0008696

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rohwer, S. (1990). Foraging differences between white and dark morphs of the Pacific Reef Heron *Egretta sacra*. *Ibis*, *132*(1), 21–26. doi:10.1111/j.1474-919X.1990.tb01012.x

Roulin, A. (2003). Geographic variation in sexual dimorphism in the barn owl *Tyto alba*: a role for direct selection or genetic correlation? *Journal of Avian Biology*, *34*(3), 251–258. doi:10.1034/j.1600-048X.2003.03022.x

Roulin, A. (2004a). Covariation between plumage colour polymorphism and diet in the Barn Owl *Tyto alba*. *Ibis*, *146*(3), 509–517.

Roulin, A. (2004b). The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews*, *79*(4), 815–848. doi:10.1017/S1464793104006487

Roulin, A., Ducrest, A.-L., & Dijkstra, C. (1999). Effect of brood size manipulations on parents and offspring in the barn owl *Tyto alba*. *Ardea*, *87*(1), 91–100.

Roulin, A., Richner, H., & Ducrest, A.-L. (1998). Genetic, environmental, and condition-dependent effects on female and male ornamentation in the barn owl Tyto alba. *Evolution*, *52*(5), 1451–1460.

Roulin, A., & Wink, M. (2004). Predator-prey relationships and the evolution of colour polymorphism: a comparative analysis in diurnal raptors. *Biological Journal of the Linnean Society*, *81*(4), 565–578. doi:10.1111/j.1095-8312.2004.00308.x

Rueffler, C., Van Dooren, T. J. M., Leimar, O., & Abrams, P. A. (2006). Disruptive selection and then what? *Trends in Ecology & Evolution*, *21*(5), 238–245. doi:10.1016/j.tree.2006.03.003

San-Jose, L. M., Séchaud, R., Schalcher, K., Judes, C., Questiaux, A., Oliveira-Xavier, A., … Roulin, A. (2019). Differential fitness effects of moonlight on plumage colour morphs in barn owls. *Nature Ecology and Evolution*, *3*(9), 1331–1340. doi:10.1038/s41559-019-0967-2

Séchaud, R., Schalcher, K., Machado, A. P., Almasi, B., Massa, C., Safi, K., & Roulin, A. (2021). Behaviour-specific habitat selection patterns of breeding barn owls. *Movement Ecology*, *9*(1), 18. doi:10.1186/s40462-021-00258-6

Skulason, S., & Smith, T. B. (1995). Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution*, *10*(9), 366–370. doi:10.1016/S0169-5347(00)89135-1

Tate, G. J., Bishop, J. M., & Amar, A. (2016). Differential foraging success across a light level spectrum explains the maintenance and spatial structure of colour morphs in a polymorphic bird. *Ecology Letters*, *19*(6), 679–686. doi:10.1111/ele.12606

Thieurmel, B., & Elmarhraoui, A. (2019). Suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.5.0, 1–10.

Tso, I. M., Tai, P. L., Ku, T. H., Kuo, C. H., & Yang, E. C. (2002). Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tetragnathidae). *Animal Behaviour*, *63*(1), 175–182. doi:10.1006/anbe.2001.1878

Tsurui, K., Honma, A., & Nishida, T. (2010). Camouflage effects of various colour-marking morphs against different microhabitat backgrounds in a polymorphic pygmy grasshopper *Tetrix japonica*. *PLoS ONE*, *5*(7), e11446. doi:10.1371/journal.pone.0011446

Tables

Table 1. Foraging strategy of male barn owls. Probability to hunt on the wing (in opposition to sit-and-wait) in relation to moonlight and owl plumage coloration, as well as temporal parameters (year, date and night duration) and number of nestlings. Results of a generalised linear mixed-effect model with a binomial distribution, including 132 male adult barn owls GPS-tracked between 2016 and 2018. The individual ID was included as random factor. Standardized estimates are provided. Significant terms are indicated in bold.

Predictors	*Estimates (SE)*	*t*	*p*
(Intercept)	-1.771 (0.117)	-15.126	**<0.001**
Plumage colour (PC)	-0.015 (0.050)	-0.308	0.758
Moonlight (M)	0.020 (0.049)	0.413	0.680
Year (2017)	-0.001 (0.144)	-0.007	0.995
Year (2018)	0.355 (0.135)	2.620	**0.009**
Date	-0.202 (0.054)	-3.742	**<0.001**
Night duration	-0.100 (0.052)	-1.922	0.055
Number of nestlings	-0.001 (0.053)	-0.024	0.981
PC x M	0.004 (0.049)	0.073	0.942

Table 2. Foraging ground selection of male barn owls. Distance to the closest forested area (square root transformed) when hunting on the wing or perched in relation to moonlight and owl plumage coloration, as well as temporal parameters (year, date and hours after dawn) and number of nestlings. Results of linear mixed-effect models including 132 male adult barn owls GPS-tracked between 2016 and 2018, with the night ID and individual ID included as random factor. Standardized estimates are provided. Significant terms are indicated in bold.

	Perching			**Hunting**		
Predictors	*Estimates (SE)*	*t*	*p*	*Estimates (SE)*	*t*	*p*
(Intercept)	14.767 (0.428)	34.499	**<0.001**	14.378 (0.450)	31.941	**<0.001**
Plumage colour (PC)	0.694 (0.226)	3.064	**0.002**	1.080 (0.244)	4.426	**<0.001**
Moonlight (M)	0.161 (0.044)	3.653	**<0.001**	0.280 (0.048)	5.804	**<0.001**
Year (2017)	-2.020 (0.190)	-10.631	**<0.001**	-1.717 (0.213)	-8.079	**<0.001**
Year (2018)	0.445 (0.276)	1.612	0.107	1.381 (0.293)	4.714	**<0.001**
Date	-25.287 (5.807)	-4.355	**<0.001**	-22.916 (6.191)	-3.702	**<0.001**
Date^2	48.754 (12.209)	3.993	**<0.001**	42.533 (13.040)	3.262	**0.001**
Date^3	-23.051 (6.493)	-3.550	**<0.001**	-19.032 (6.947)	-2.740	**0.006**
Hours after dawn	-1.189 (0.148)	-8.055	**<0.001**	-1.938 (0.163)	-11.881	**<0.001**
Hours after dawn^2	0.861 (0.149)	5.798	**<0.001**	1.607 (0.165)	9.765	**<0.001**
Number of nestlings	0.394 (0.095)	4.159	**<0.001**	0.219 (0.099)	2.214	**0.027**
PC x M	0.018 (0.046)	0.397	0.691	0.098 (0.050)	1.951	**0.048**

Table 3. Prey species captured by male barn owls. Probability to capture the two main barn owl prey, *Apodemus* sp. and *Microtus arvalis*, in relation to moonlight and owl plumage coloration, as well as temporal parameters (year, date and hours after dawn) and number of nestlings. Results of generalised linear mixed-effect models with binomial distributions, including 3’364 prey captured in 77 different nests. The night ID and individual ID were included as random factor. Standardized estimates are provided. Significant terms are indicated in bold.

	***Apodemus* sp.**			***Microtus arvalis***		
Predictors	*Estimates (SE)*	*t*	*p*	*Estimates (SE)*	*t*	*p*
(Intercept)	-2.953 (0.272)	-10.860	**<0.001**	1.833 (0.204)	9.000	**<0.001**
Plumage colour (PC)	0.359 (0.148)	2.427	**0.015**	-0.243 (0.134)	-1.816	0.069
Moonlight (M)	-0.128 (0.070)	-1.822	0.068	0.104 (0.055)	1.884	0.060
Year (2017)	1.300 (0.299)	4.344	**<0.001**	-0.904 (0.223)	-4.051	**<0.001**
Year (2018)	0.888 (0.339)	2.618	**0.009**	-0.632 (0.269)	-2.350	**0.019**
Date	-0.340 (0.124)	-2.734	**0.006**	0.175 (0.101)	1.726	0.084
Hours after dawn	0.106 (0.058)	1.834	0.067	-0.024 (0.047)	-0.519	0.604
Number of nestlings	0.064 (0.130)	0.488	0.626	-0.163 (0.122)	-1.335	0.182
PC x M	-0.026 (0.079)	-0.330	0.742	0.121 (0.059)	2.063	**0.039**

Figures

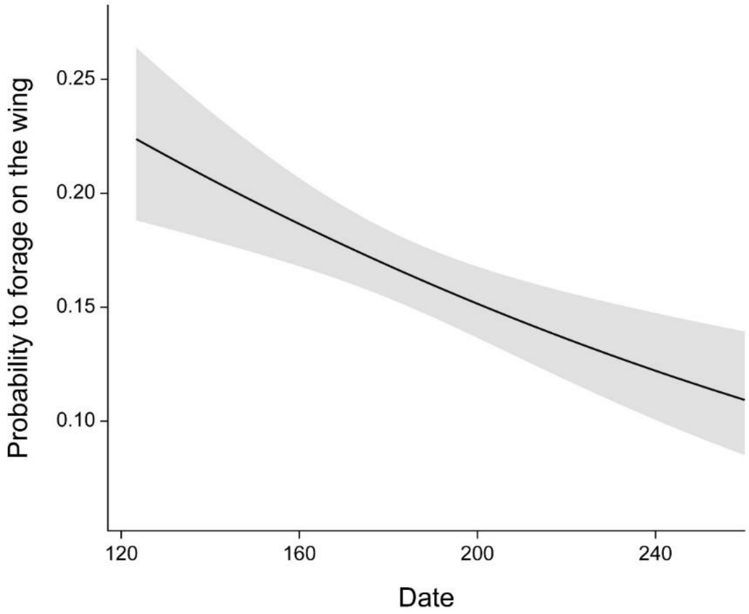


Figure 1. Male barn owl's foraging strategy in relation to the date. The continuous line represents the probability to forage on the wing (*vs.* perched), and the grey area the 95% confidence intervals associated (from the model reported in Table 1).

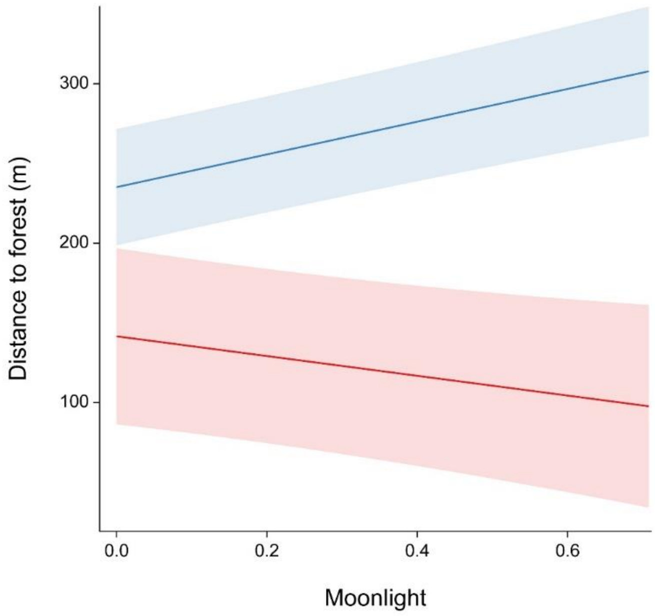


Figure 2. Male barn owl's distance to the forest when hunting on the wing, in relation its plumage colouration and moon illumination. The continuous lines represent the predicted distance to the forest, and the shaded areas the 95% confidence intervals associated (from the model reported in Table 2). The blue line represents white owls (colour score=8) and the red line represents reddish owls (colour score=1).

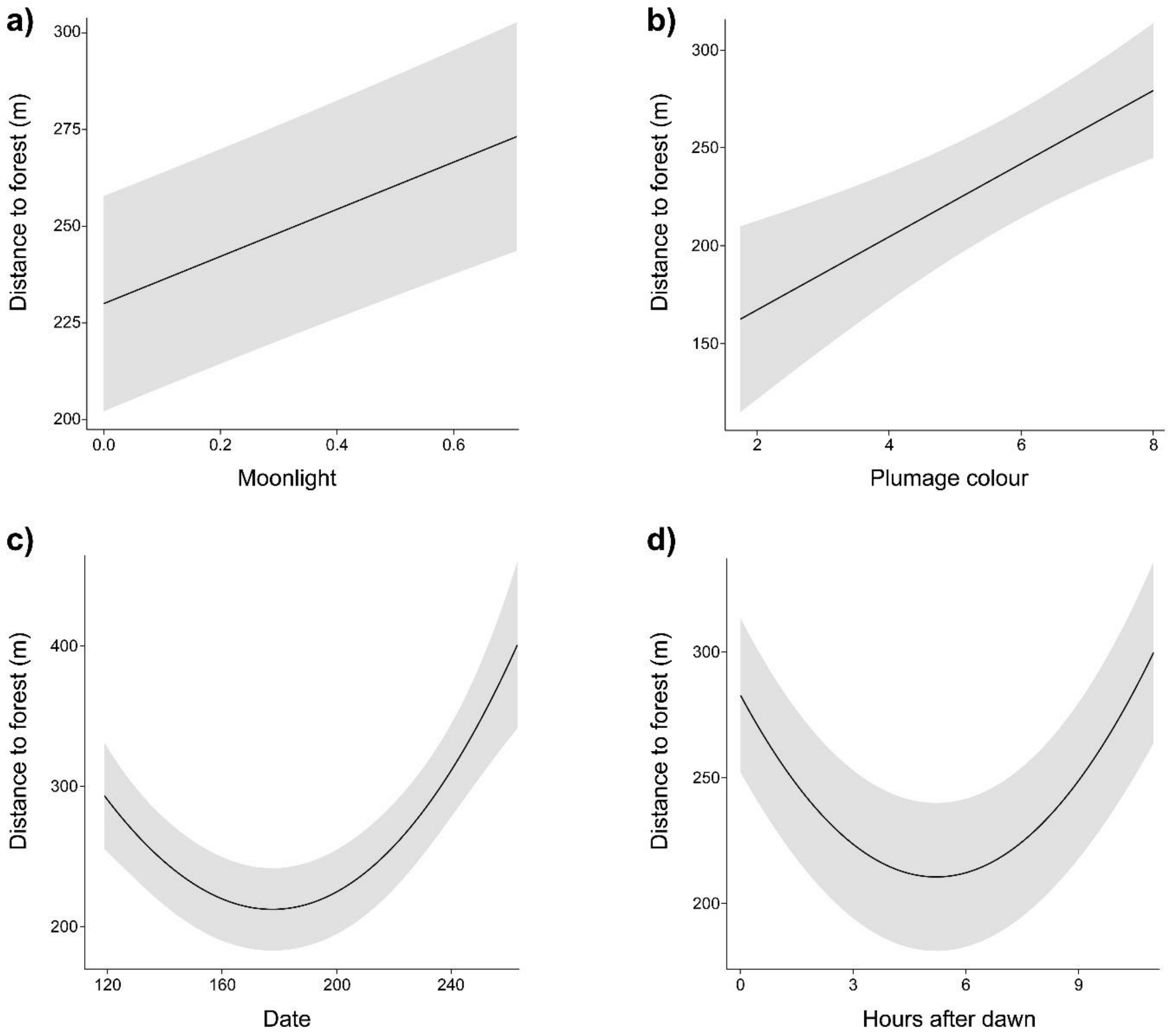


Figure 3. Male's foraging distance from the forest in relation to a) the moon illumination, b) its plumage colouration, c) the date, and d) the number of hours after dawn. Results plotted here are for the hunting on the wing foraging strategy, but results for hunting perched are similar (see models reported in Table 2). The continuous lines represent the predicted distance data, and the shaded areas the 95% confidence intervals associated.

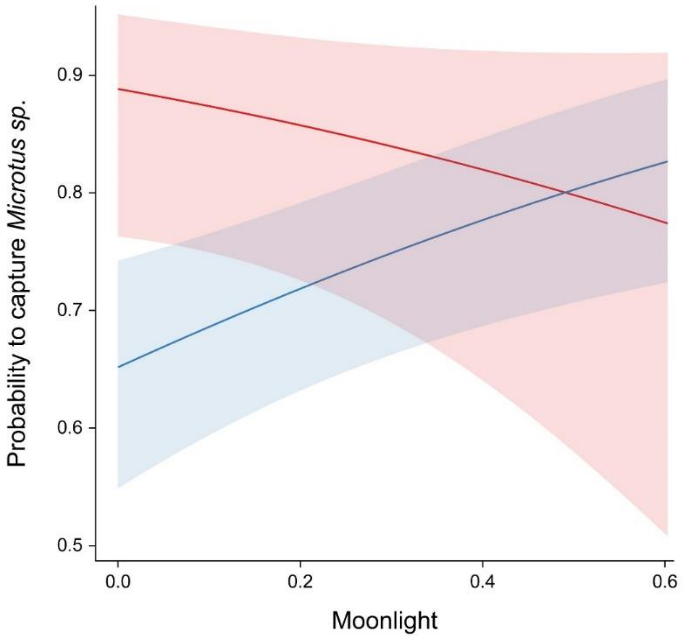


Figure 4. Male barn owl's probability to prey on common voles *Microtus arvalis* in relation to its plumage colouration and moon illumination. The continuous lines represent the predicted values, and the shaded areas the 95% confidence intervals associated (from the model reported in Table 3). The blue line represents white owls (colour score=8) and the red line represents reddish owls (colour score=1).

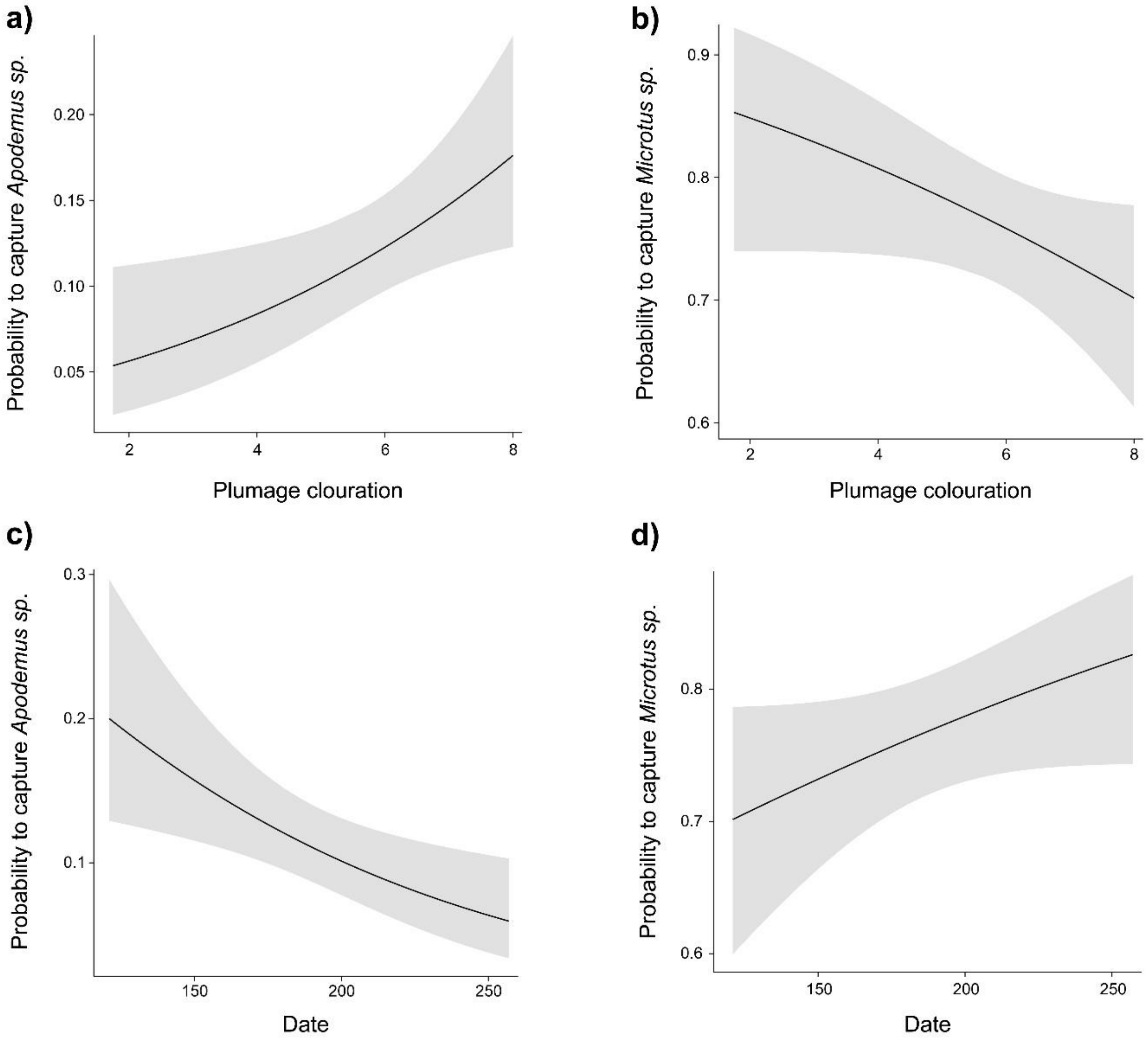


Figure 5. Male barn owl's prey capture. Plumage colouration (panels a and b) and date (panels c and d) on the probability to prey on wood mice *Apodemus* sp. and common voles *Microtus arvalis*. The continuous lines represent the predicted values, and the shaded areas the 95% confidence intervals associated (from the model reported in Table 3).

Chapter 4 – Supplementary information

Table S1. The relative importance of the parameters included in the dredge model. We ran one model per owl's sex and behavioural mode (perching or hunting), and we considered two different plumage colour parameters as covariate (average colouration and morph, see the "Material and Methods" section for details). Models with ΔAICc<6 were averaged, and the importance weights of each variable extracted. The colour gradient ranges from red (0 = low importance) to green (1 = high importance).

	COLOUR MODEL				**MORPH MODEL**			
	Perching		**Hunting**		**Perching**		**Hunting**	
	Male	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**
Colouration parameter (CP)	1	1	1	0.63	1	0.61	1	0.6
Moon illumination (MI)	1	1	1	1	1	1	1	1
Year	1	1	1	1	1	1	1	1
Date	1	1	1	1	1	1	1	1
Date^2	1	1	1	1	1	1	1	1
Date^3	1	1	0.96	0.35	1	1	0.7	0.33
Hours after sunset	1	0.78	1	1	1	0.78	1	1
Hours after sunset^2	1	0.7	1	1	1	0.7	1	1
Hours after sunset^3	0.51	0.19	0.54	0.29	0.51	0.19	0.55	0.28
Number of nestlings	1	1	0.82	1	1	1	0.31	1
CP x MI	0.28	0.25	0.72	0.46	0.26	0.46	0.56	0.6
Number of models averaged	4	12	10	12	4	12	16	7

Table S2. The moon illumination was estimated based on three different formulas used in recent literature (see the "Material and Methods" section for details). We compared these estimations (and three transformations: square-root, quadratic and cubic) to the night luminance measured on the ground at a meteorological station in the center of the study area (Payerne; 46°49'13.888"N 6°56'13.792"E). The moon illumination data obtained with the second formula (fraction + presence + elevation) at the power two and three were best approximated the measured values. For simplicity, the squared value has been kept in the following analyses.

Moon illumination	Variable transformation	AIC	Δ AIC	Adjusted r^2
fraction + presence	X	72270.91	4329.81	0.337
	$X^{0.5}$	71993.54	4052.44	0.362
	X^2	71891.17	3950.07	0.371
	X^3	71791.79	3850.69	0.379
fraction + presence + altitude	X	67973.37	32.27	0.631
	$X^{0.5}$	67950.83	9.73	0.632
	X^2	67942.55	1.45	0.632
	X^3	67941.1	0	0.633
fraction + presence + altitude + TTC	X	72530.03	4588.93	0.314
	$X^{0.5}$	72329.31	4388.21	0.332
	X^2	72483.04	4541.94	0.318
	X^3	72424.41	4483.31	0.324

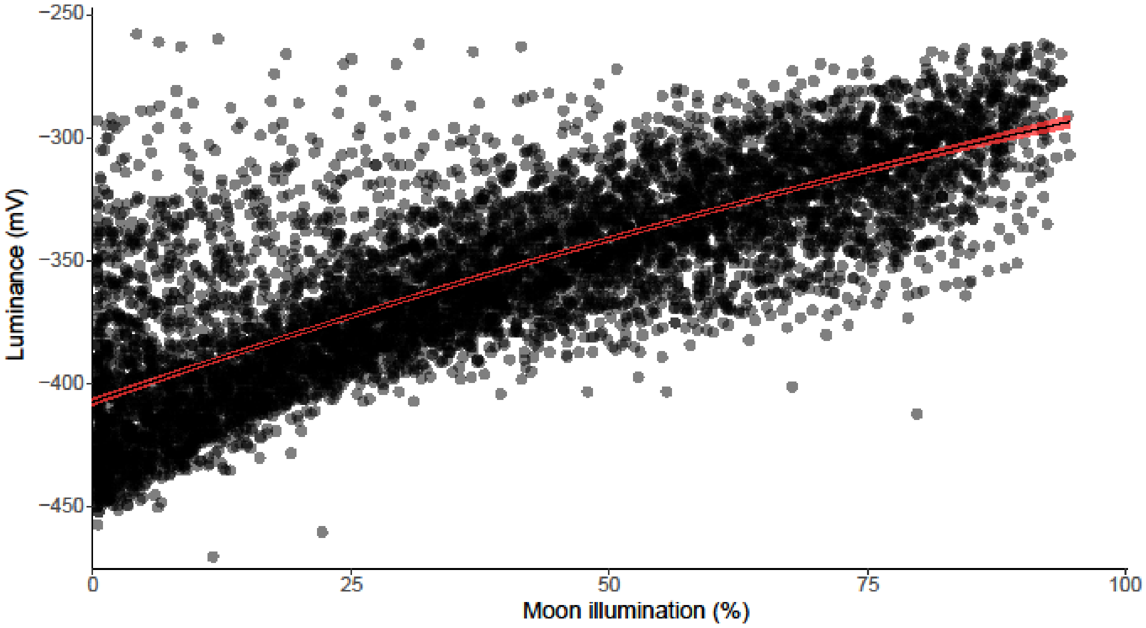


Figure S1. Relationship between the moon illumination and the night luminance measured on the ground. The Moon illumination was estimated using the moon's presence, visible fraction and elevation above the horizon (see formula in Pajot et al. 2021). The night luminance was obtained from a MeteoSwiss meteorological station in the study area (Payerne; 46°49'13.888"N 6°56'13.792"E). The squared-value of moon illumination fitted better the luminance values (see table S2) and was thus used in the analyses.

Chapter 5

Climate-driven convergent evolution of plumage colour in a cosmopolitan bird

Andrea Romano[1], Robin Séchaud[1], Alexandre H. Hirzel[2] and Alexandre Roulin[1†]

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

[2] Centre Informatique, University of Lausanne, Lausanne, Switzerland

Chapter Status:

Published in Global Ecology and Biogeography

https://doi.org/10.1111/geb.12870

Author contributions:

A.R., A.R.† conceived the study; A.R.† collected the data; A.R., R.S. and A.H.H. performed the statistical analyses; A.R. drafted the manuscript; all the authors contributed to the final version of the paper.

Received: 20 June 2018 | Revised: 11 October 2018 | Accepted: 29 October 2018
DOI: 10.1111/geb.12870

RESEARCH PAPER

WILEY Global Ecology and Biogeography A Journal of Macroecology

Climate-driven convergent evolution of plumage colour in a cosmopolitan bird

Andrea Romano[1] | Robin Séchaud[1] | Alexandre H. Hirzel[2] | Alexandre Roulin[1]

[1]Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

[2]Centre Informatique, University of Lausanne, Lausanne, Switzerland

Correspondence
Andrea Romano, Department of Ecology and Evolution, University of Lausanne, Building Biophore, Lausanne CH-1015, Switzerland.
Email: andrea.romano@unil.ch

Funding information
Fondation du 450eme anniversaire; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 31003A_153467; American Natural History Museum; Fondation Agassiz, Université de Lausanne; Akademie der Naturwissenschaften; Basler Stiftung fur biologische Forschung

Editor: Adriana Ruggiero

Abstract

Aim: The investigation of phenotypic diversity across geographical gradients is pivotal to understanding the evolution and adaptive functions of alternative phenotypes. The aim of the present study was to investigate whether the polymorphism in ventral plumage colouration observed in the cosmopolitan common barn owl group is determined by climatic factors, such as temperature and rainfall, consistent with Gloger's and Bogert's biogeographical rules.

Location: World.

Time period: 1809–2017.

Major taxa studied: *Tyto alba* species complex.

Methods: We analysed the variation in heritable melanin-based plumage colour according to annual temperature and rainfall in 9,110 individuals of the cosmopolitan barn owl, with three distinct evolutionary lineages representing its entire distribution range: the Afro-European *Tyto alba*, occurring between Scandinavia and South Africa, the American *Tyto furcata*, found from southern Canada to Patagonia, and the Australasian *Tyto javanica*, living between the Himalayan Plateau and Tasmania.

Results: Although the geographical distribution of colour morphs is heterogeneous among the lineages, in all of them plumage colour becomes darker with increasing annual rainfall, indicating a convergent selection of darker morphs in humid habitats possibly to improve camouflage against the dark environment and/or to repel water more efficiently. Moreover, in *T. alba* and *T. furcata*, melanization increases at decreasing temperature, suggesting its possible role in thermoregulation.

Discussion: These findings provide convincing evidence of repeated evolution of similar body colouration patterns at a worldwide scale compatible with the main biogeographical rules, while emphasizing the possible role of melanin-based traits in animal adaptation to climate change.

KEYWORDS
adaptive radiation, biogeographical rules, convergent evolution, cosmopolitan species, melanin colour, natural selection

1 | INTRODUCTION

Ecological and climatic factors dramatically vary not only at large geographical scales, such as among continents, but also at smaller scales. This can explain the origin and maintenance of phenotypes adapted to local conditions (Huey, Gilchrist, Carlson, Berrigan, & Serra, 2000), which in turn might be preludes to ecological speciation events (Barton, 2010). While basic thermoregulation principles can explain the geographical variation in body features, such as size and shape of body appendages, which has been documented in many species (Allen, 1877; Bergmann, 1847), identifying the evolutionary pressures causing spatial polymorphisms in animal colouration has been proven to be more elusive. Colouration has multiple functions, from cryptic background matching and camouflage promoted by predator–prey interactions to conspicuous visual signals emerging as the result of sexual and social selection (Cuthill et al., 2017). Colour patterns are therefore driven by various, often opposing, selective forces, and thus represent compromises between such conflicting pressures acting locally (Cuthill et al., 2017). Because the strength of distinct selective pressures varies among habitats due to differences in climate and/or lighting conditions (Hill & McGraw, 2006; Passarotto, Parejo, Penteriani, & Avilés, 2018) and exposure to parasites and predators, as well as in breeding strategies and sexual behaviour (Cuthill et al., 2017; Hill & McGraw, 2006), geographical colour polymorphisms can arise.

This complex evolutionary scenario is further complicated by the existence of pleiotropic effects of genes responsible for the synthesis of pigments, such as melanin, on physiological and behavioural traits that can have crucial effects upon individual fitness (Ducrest, Keller, & Roulin, 2008; Roulin & Ducrest, 2011). Melanin is the pigment responsible for light-to-dark colour variation in animals, and its variation has been associated with many organismal traits and functions (Ducrest et al., 2008; Roulin & Ducrest, 2011). Selective advantages of a given colour morph can therefore arise locally as the by-product of selection in favour of individuals displaying other adaptive phenotypic traits genetically linked to colouration.

Two main biogeographical rules have been proposed to explain both intraspecific and interspecific variation in pigmentation according to climatic factors. On the one hand, Gloger's rule predicts that more humid, warm and vegetated environments should host darker animals compared to more dry and open habitats (Delhey, 2017; Gloger, 1833). On the other hand, Bogert's rule, or the "thermal melanism rule", postulates that animals inhabiting colder areas should be darker coloured, because they gain a thermal advantage comparing to paler individuals as a consequence of greater absorption of solar radiation (Bogert, 1949; Trullas, van Wyk & Spotila, 2007). These rules have been verified in a large variety of animals, spanning from insects (Bishop et al., 2016; Mayr, 1963) to birds (Burtt & Ichida, 2004; Delhey, 2017, 2018; Friedman & Remeš, 2016; Galvan, Rodríguez-Martínez, & Carrascal, 2018; Zink & Remsen, 1986) and mammals (Caro, 2005; Kamilar & Bradley, 2011; Nigenda-Morales, Harrigan, & Wayne, 2018; Stoner, Caro, & Graham, 2003). In birds in particular, geographical variation in plumage colour compatible with these two biogeographical rules has been shown both at the within-species level (Roulin & Randin, 2015; Zink & Remsen, 1986) and in comparative studies (Delhey, 2018; Friedman & Remeš, 2016; Passarotto et al., 2018). However, no study has investigated its occurrence at the global scale.

In the present study, we examined the variation in two melanin-based plumage traits (breast pheomelanin-based colouration, and size of black eumelanic feather spots) in relation to geographical and climatic factors in 9,110 specimens of three distinct evolutionary lineages of the common barn owl group (the Afro-European or Western barn owl *Tyto alba*, the American barn owl *Tyto furcata* and the Australasian or Eastern barn owl *Tyto javanica*; Uva, Päckert, Cibois, Fumagalli, & Roulin, 2018) across their entire range of distribution (Supporting Information Figure S1). Irrespective of the taxonomic status of these evolutionary units (see 2.1 Study system), they can be considered as adaptive radiations occurring "simultaneously" in different regions and producing a wide range of local adaptations, thus providing the unique opportunity to disclose whether the same climatic/biogeographical factors promoted the evolution of convergent colour polymorphism in different areas. The body underside varies from white to reddish-brown and from immaculate to heavily marked with black spots of variable size (Figure 1), both among and within populations (Roulin, 2003). In all populations, females are, on average, darker coloured and display bigger black spots than males (Roulin, 2003).

We first describe the geographical variation in the two melanin-based plumage traits to examine whether the degree of melanism varies with latitude and between hemispheres. In addition, because plumage traits can differ between insular and continental populations (Roulin & Salamin, 2010), we also investigated whether owls located on islands or mainland are differently pigmented. We then investigated whether the observed colour patterns can be explained by climatic factors (temperature, rainfall) and whether the geographical colour polymorphisms are compatible with the aforementioned biogeographical rules. Under a scenario of convergent evolution during concomitant adaptive radiations, we expected similar relationships between colour traits and climatic factors among Western, American and Eastern barn owls.

FIGURE 1 An example of the variation in plumage colouration and spot size in a population of the Western barn owl breeding in Switzerland. Barn owls display continuous variation in plumage colouration from immaculate white to dark reddish pheomelanic, as well as exhibiting a different number of eumelanic spots of variable size [Colour figure can be viewed at wileyonlinelibrary.com]

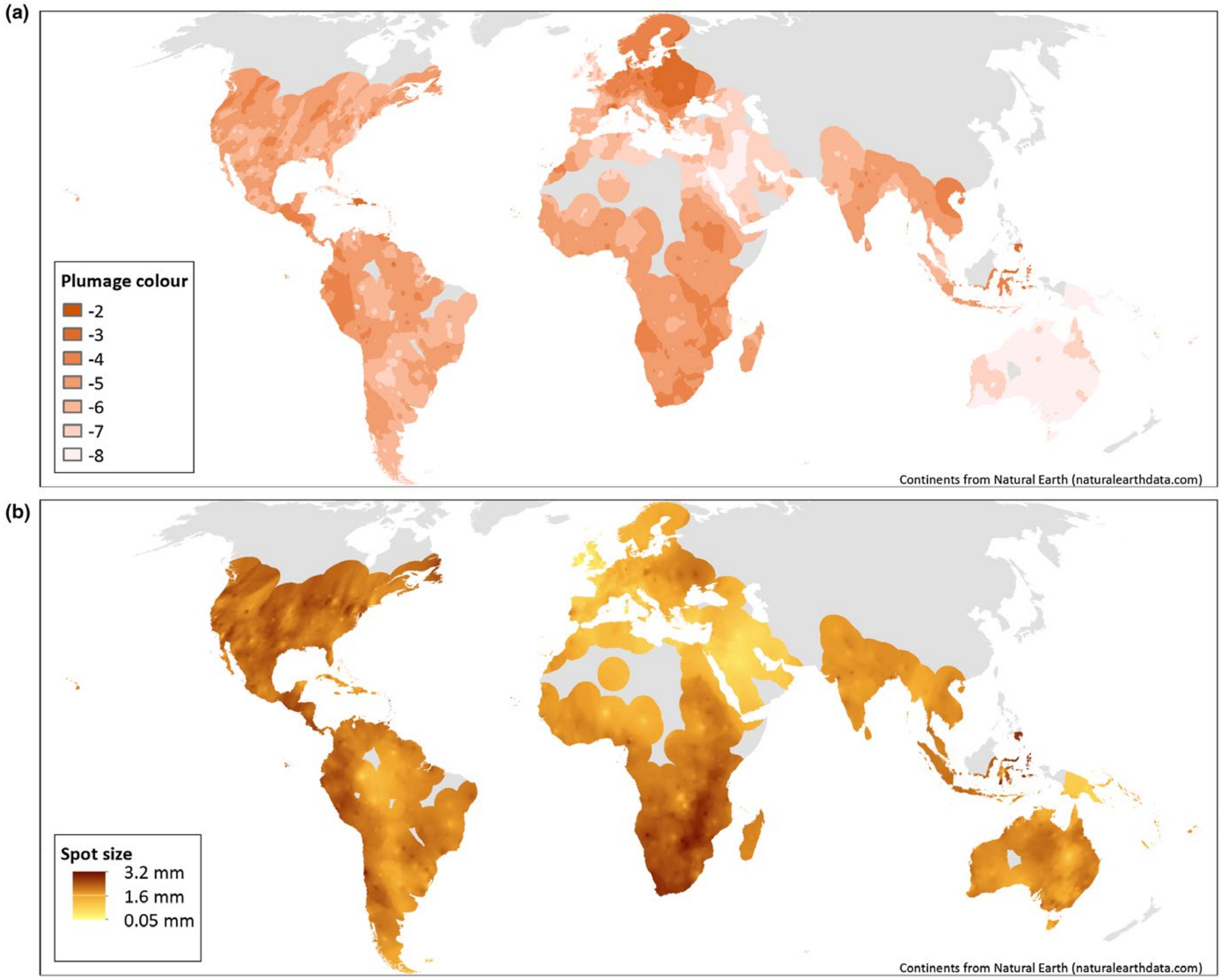


FIGURE 2 Geographical variation in plumage colour (a) and spot size (b) in the common barn owl group, the Western barn owl (*Tyto alba*), the American barn owl (*Tyto furcata*) and the Eastern barn owl (*Tyto javanica*). The three evolutionary lineages inhabit geographically separated ranges [Colour figure can be viewed at wileyonlinelibrary.com]

2 | METHODS

2.1 | Study system

The common barn owl group (also known as the *T. alba* species complex) is a group of nocturnal owls (König & Weick, 2008), occurring in all the continents except Antarctica (Figure 2). It can exploit a wide range of habitats, from open landscapes like deserts and grasslands to temperate and tropical forests, thus allowing it to occur across a huge latitudinal range (from *c.* 65°N to *c.* 55°S; Figure 2) and to occupy very remote areas, including most of the world's archipelagos (e.g., the Falkland and Bermuda islands in the Atlantic Ocean; Galapagos, Vanuatu and Tonga islands in the Pacific Ocean; Seychelles and Andaman islands in the Indian Ocean). Although the morphology of common barn owl group populations is globally similar, discrete differences in body size, plumage colouration and geographical distribution have led to various classifications of this taxon into different numbers of species, spanning from a single polytypic species to four separate species, including a variable number of subspecies worldwide (up to 36 depending on the criteria used; see Uva et al., 2018 for details). However, most of the previously recognized subspecies were not supported by a recent comprehensive molecular phylogeny carried out on nuclear and mitochondrial markers (Uva et al., 2018). Individuals that were considered to belong to distinct, geographically distant subspecies were in many cases more genetically related to each other than individuals sampled in the same population (Uva et al., 2018). This result indicates that different colour morphs can result from local adaptations as the product of recent selection favouring a given phenotype rather than as a consequence of a common genetic background.

The correct taxonomy of the common barn owl group is therefore far from being fully elucidated (Uva et al., 2018). However, all the phylogenetic reconstructions available to date (Aliabadian, Alaei-Kakhki, Mirshamsi, Nijman, & Roulin, 2016; Uva et al., 2018; Wink, El-Sayed, Sauer-Gürth, & Gonzalez, 2009) are coherent in agreeing that this species complex is divided into three genetically distinct evolutionary lineages, which irrespective of taxonomic status can be considered as adaptive radiations occurring simultaneously in different geographical regions: the Western (or Afro-European) barn owl (*T. alba*), occurring from southern Scandinavia to South Africa, the American barn owl (*T. furcata*), from southern Canada to Patagonia, and the Eastern (or Australasian) barn owl (*T. javanica*), from the Himalayan plateau to Tasmania (Figure 2; Supporting Information Figure S1).

2.2 | Museum skins collection

Plumage data were extracted from 9,110 barn owl skins (3,580 males, 3,863 females, 1,667 unsexed individuals) collected between the years 1809 and 2017 by 141 museums and private citizens across the world (Supporting Information Appendix). Skins originate from the entire range of distribution of the common barn owl group, and belong to 4,670 Western, 3,050 American and 1,390 Eastern barn owls (Supporting Information Appendix, Figure S1). The degree of reddish colouration of the breast was categorized on an eight-level scale, ranging from 1 for dark red to 8 for white. This method is highly reliable for describing the variability of the background feather colour observed in the species because it is strongly correlated with reflectance in the range of visible light as measured by spectrometric procedures (Dreiss & Roulin, 2010).

The diameter of a representative average black spot was measured to the nearest 0.1 mm using a calliper. To test whether the method of measuring the diameter of black spots is reliable, we calculated the repeatability in spot size on 199 individuals breeding in Switzerland between 1994 and 2016 that were measured twice during the same breeding season (range difference between the two measurements: 3–134 days). The repeatability is very high (intra-class correlation coefficient = 0.85; Confidence Interval 95% = 0.81–0.89; see also Roulin, Uva, & Romano, 2018).

For each individual, information about its sex was included, but only if this was reported on the label of the museum specimen or if it was possible to identify the sex depending on traits other than the plumage colour. Although sexual dichromatism is common in the barn owl group, when information about sex was lacking we could not infer if a given specimen was a male or a female depending only on its plumage traits because large within-sex colour variability also exists, males possibly displaying a female-like phenotype and vice versa (Roulin & Jensen, 2015). All the analyses were thus run including all the available individuals (i.e., excluding the effect of sex in the models) and on a subsample of specimens for which sex was known (see Supporting Information).

Two out of the three barn owl evolutionary lineages considered here, namely *T. furcata* and *T. javanica*, have been suggested to be paraphyletic. According to the most comprehensive and accurate phylogenetic analysis, the ashy-faced owl (*Tyto glaucops*) from Hispaniola, including the formerly identified subspecies *Tyto g. nigrescens* and *Tyto g. insularis*, is embedded within the American lineage (Uva et al., 2018). The same is the case for *Tyto rosenbergii* and *Tyto nigrobrunnea*, endemic to Sulawesi and Taliabu island, respectively, which are both nested within the Eastern barn owl evolutionary lineage (Uva et al., 2018). This result suggests that these three morphologically distinct taxa (*T. glaucops*, *T. rosenbergii*, *T. nigrobrunnea*), all characterized by limited and insular distribution, diverged only recently from their specific lineage of the barn owl group and/or that gene flow is still occurring. Nevertheless, in an adaptive radiation scenario such as hypothesized in the present study, we cannot discard the possibility that they might be cases of recent island adaptations driven by local peculiar climatic conditions. For this reason, we preferred to also include in the analyses the individuals belonging to these three taxa (118 *T. glaucops*, 62 *T. rosenbergii* and 1 *T. nigrobrunnea* specimens; Supporting Information Appendix). However, the analyses were also run excluding them in order to verify that their inclusion did not affect the results (see Supporting Information).

2.3 | Climatic data

Recovery location, as reported on the label of each museum specimen, was converted into geographical coordinates (Supporting Information Figure S1). When the exact location was not reported (e.g., "specimen collected near a given city"), we assigned coordinates near the centre of the specified region (or small country). However, we discarded all the individuals for which the recovery site was not precise enough to establish accurate coordinates (e.g., when the label reported that the specimen was collected in a large country). When more than one individual originated from the same area, we assigned them slightly different coordinates (distance 1–5 km) to be considered as independent observations. We consider this procedure accurate because barn owls are territorial birds, with a home range of up to 3,175 ha (Colvin, 1985), and because individuals from the same area were collected in different years.

For each pair of coordinates, we collected climatic information from the Worldclim dataset for the period 1970–2000 (http://www.worldclim.org/) at a 30 arc-second spatial resolution, corresponding to about 1 km^2. The barn owl is a non-migratory species, spending the entire year in the same region. Values of the mean annual temperature and mean total annual rainfall were therefore associated with each individual. However, it is a moderately vagile species that can forage at a distance up to 5–6 km from its nest (Brandt & Seebass, 1994) and spends its non-breeding period across a range four times larger than that in the breeding season (Cayford, 1992; Souza, Asfora, Lira, & Astúa, 2010), potentially using different neighbouring habitats. In order to account for the possible heterogeneity of the habitats exploited by each individual during its life, we also computed mean annual temperature and mean total rainfall over radii of 20 and 50 km from the location where the specimen was collected. This approach also enabled us to control for potential small errors in the identification of the recovery site reported in the museum labels, and when the information on the specimen recovery location was not accurate. We note that the climatic data for the recovery location and over the 20- and 50-km radii were strongly correlated (temperature: $r > 0.97$; rainfall: $r > 0.96$). Because the analyses at these different spatial scales provided very similar results, in the Results section we only present the output concerning the intermediate value (i.e., 20-km radius; other details not shown).

The period for which climatic data were extracted (1970–2000) is different from the timespan when the owls were collected (1809–2017). Unfortunately, we are not in the position to re-run the analyses on the same time windows for which we have the climatic data because of the huge reduction in sample size (from 9,110 to 2,843 specimens), probably because in the past it was much easier to kill and collect animals. Moreover, the reduction in sample size is not similar across the globe, thus considerably reducing the locations included in our dataset, and preventing proper analysis of the worldwide variation in colour traits. However, we note that even though climate changed during the last century, similar climatic differences have persisted between regions. This is the case because for the locations included in our analyses the correlation between the current temperature and the mean temperature recorded in various time windows spanning between 20,000 and 2,000 years ago is always larger than 0.92, thus indicating that it is valid to use the 1970–2000 climatic data to investigate whether barn owl plumage evolution was determined by climate or linked factors.

2.4 | Statistical analyses

To investigate colour variation according to geographical and climatic factors, we relied on generalized least squares (GLS) methods accounting for spatial autocorrelation between datapoints, run with the *nlme* package (Pinheiro, Bates, DebRoy, Sarkar, & the R Core Team, 2014) in R (version 3.5.1). Variation in breast plumage colour and spot size was tested separately for the Western, American and Eastern barn owl lineages in two sets of analyses, including as predictors: (a) hemisphere and absolute latitude of the recovery location and their interaction (*geographical* models); (b) mean annual temperature, total annual rainfall and their interaction (*climatic* models). In the *climatic* models, a square root conversion of annual rainfall values was performed to generate a normal distribution. To obtain scale-independent estimates of the covariation between colour traits and continuous predictors and to compare results of different lineages, all continuous climatic covariates were standardized within each taxon. This approach was chosen to account for the variation in climatic factors in the geographical range where each lineage evolved as it uses only the ranges of temperature and precipitation to which each lineage was exposed to during its adaptive radiation. However, qualitatively very similar results were obtained when climatic variables were standardized using data for the three lineages pooled (details available upon request). Because it has been shown that plumage traits can differ between insular and continental populations (Roulin & Salamin, 2010), a dichotomic factor indicating if the specimen originated from an island (coded as 1) or from the mainland (including Australia; coded as 0) was also added to all models. In the *climatic* models of a given plumage trait (e.g., spot size) we also included the other plumage trait (i.e., plumage colour) as predictor. This procedure allowed us to test for variation in one trait while also accounting for the concomitant variation in the other genetically linked trait (Roulin & Jensen, 2015). Finally, as phenotypes can be hypothesized to vary with temperature in a nonlinear way, we also included the quadratic term of annual temperature, which was subsequently excluded from all the final models for never having attained statistical significance (details not shown). Non-statistically significant interaction terms were also removed from final models.

All analyses accounted for spatial autocorrelation by including a Gaussian spatial correlation structure (Züur et al., 2009). As spatial autocorrelation was different between plumage traits and barn owl lineages (see Figure 2), we included a specific correlation matrix (reflecting the correlation between each pair of datapoints in relation to their distance) for each model independently. The correlation structure of every model was generated using the CorRGaus procedure with the R package *ramps* (Smith, Yan, & Cowles, 2008) by assessing the "range" value after exploring the variogram of the residuals of any given model without accounting for spatial dependence of datapoints (Züur et al., 2009). The great-circle distance between longitude/latitude coordinates, expressed in km, was computed by setting the "haversine" metric. As expected considering the high variability in plumage colour traits among individuals inhabiting nearby locations, in all variograms we observed a moderate-to-large nugget effect. Each correlation matrix was therefore weighted by its associated nugget effect by multiplying all the values in the correlation matrix by 1 minus the nugget effect. Finally, the resultant correlation matrix was converted into a correlation structure (corsym) to be compatible with the GLS models. To verify that this procedure resulted in the removal of spatial autocorrelation, a variogram of the residuals of each final model was produced (Supporting Information Figure S2). In all cases, final models showed no spatial dependence of residuals (Supporting Information Figure S2), and the Akaike's information criterion (AIC) of each model considerably improved (Supporting Information Table S1).

For the sake of comprehensiveness, *climatic* models including the same predictors described above were run on data of Western, American and Eastern barn owls pooled together. These models included the additional effect "lineage", in order to pool data belonging to the three distinct evolutionary units. In these analyses, we did not account for the phylogenetic relationships among the lineages because of the small number of evolutionary units and because this information was partly included in the spatial correlation structure (see also Roulin, Wink, & Salamin, 2009). However, we note that these models can be considered as a corollary of the main analyses performed separately between the different evolutionary lineages of the common barn owl group.

As mentioned above, all the models were performed on all the individuals and only on the subset of specimens for which the sex was known. Considering that in darker populations both males and females are coherently darker than individuals of the same sex living in light-plumaged populations (Roulin, Dijkstra et al., 2001) and that geographical clines in plumage colour seem to be similar between the sexes (Roulin, 2003), in order not to complicate the analyses we did not test for the effect of the interaction between sex and climatic variables. In addition, the *climatic* models were also performed both including and excluding data of the three distinct morphological taxa that were formerly described as distinct species on the basis of morphological criteria (*T. glaucops*, *T. rosenbergii* and *T. nigrobrunnea*). On the whole, with a few exceptions, the same model performed on different subsamples provided qualitatively similar results. In the main text, we report the results of the analyses performed on the largest sample size, while the other ones are shown in Supporting Information Tables S2–S4. All the *climatic* models were re-run including the fixed effect of hemisphere and all the results were qualitatively similar (details not shown). However, the models were not re-run with absolute latitude as a fixed effect because of its high correlation with climatic predictors (e.g., correlation between absolute latitude and temperature: $-0.75 < r < -0.88$; $p < 0.0001$ in the three lineages) and because this information was already included in the spatial autocorrelation matrices. Finally, to check the robustness of our results, all the analyses were performed assuming increasing scales of spatial autocorrelation (i.e., different "ranges"), and always provided qualitatively similar results (see Supporting Information Table S5 for an example). In the Results section we always provide the details of the model with the smallest AIC.

3 | RESULTS

3.1 | Geographical variation in plumage traits

The different lineages of the common barn owl group show heterogeneous geographical variation in both plumage traits (Figure 2). In the Afro-European barn owl, plumage colour is significantly darker on the mainland than on islands. No significant variation according to hemisphere, latitude (Table 1; Supporting Information Table S2, Figure S3) or their interaction ($t = 0.83$; $p = 0.41$) is observed. In the American barn owl, plumage colour does not vary in relation to hemisphere, and is darker with decreasing latitude, that is, closer to the Equator (Table 1, Figure S3). However, the latter relationship is not significant when the analysis is performed on the subsample of the sexed individuals (Supporting Information Table S2). No significant effect of the hemisphere by latitude interaction was detected ($t = 1.57$; $p = 0.17$; Supporting Information Figure S3, Table S2). In the Australasian barn owl, populations living at higher latitudes display on average a lighter plumage (Table 1; Supporting Information Table S2, Figure S3). Nevertheless, in this lineage, differential variation in plumage colour with latitude is observed in different hemispheres: in the Southern Hemisphere, plumage colour is significantly darker close to the Equator, while the opposite holds true for the Northern Hemisphere (hemisphere by latitude interaction: $t = 3.37$; $p < 0.001$; Table 1; Supporting Information Table S2, Figure S3).

Different geographical patterns of variation in spot size emerges among the three evolutionary lineages (Figure 2). In the Western barn owl, spot size is significantly larger in the Southern Hemisphere, and it significantly decreases with latitude (Table 1; Supporting Information Table S2, Figure S4). In addition, variation in spot size with latitude differs between the hemispheres: it significantly increases with latitude in the Southern Hemisphere, while in the Northern Hemisphere spot size is larger close to the Equator and reaches its smallest value at high latitudes (hemisphere by latitude interaction: $t = 4.07$; $p < 0.001$; Table 1; Supporting Information

TABLE 1 Variation in plumage colour and spot size according to absolute latitude, hemisphere and island versus mainland in the three lineages of the common barn owl group

	Plumage colour			Spot size		
	Coefficient (*SE*)	***t***	***p***	**Coefficient (*SE*)**	***t***	***p***
Western barn owl (*Tyto alba*)						
Intercept	5.318 (0.535)			10.806 (1.413)		
Island	**0.604 (0.142)**	**4.25**	**0.017**	**−2.079 (0.527)**	**3.94**	**<0.001**
Absolute latitude	0.006 (0.009)	0.61	0.54	**−0.119 (0.023)**	**5.21**	**<0.001**
Hemisphere	−0.543 (0.297)	1.83	0.07	**7.457 (0.775)**	**9.62**	**<0.001**
American barn owl (*Tyto furcata*)						
Intercept	4.021 (0.389)			24.006 (1.846)		
Island	0.044 (0.185)	0.24	0.81	**−2.005 (0.609)**	**3.37**	**<0.001**
Absolute latitude	**0.016 (0.007)**	**2.23**	**0.026**	**−0.034 (0.035)**	0.96	0.34
Hemisphere	0.255 (0.211)	1.21	0.27	1.745 (0.962)	1.81	0.07
Eastern barn owl (*Tyto javanica*)						
Intercept	4.408 (0.744)			20.863 (2.184)		
Island	0.180 (0.197)	0.91	0.36	**−2.181 (0.838)**	**2.60**	**0.009**
Absolute latitude	**0.046 (0.021)**	**2.13**	**0.033**	−0.091 (0.059)	1.54	0.12
Hemisphere	0.400 (0.372)	1.08	0.28	−0.305 (1.190)	0.26	0.80

Note. The effects of the interaction between absolute latitude and hemisphere are reported in the main text. Bold type indicates statistical significance. Residual degrees of freedom: *T. alba* colour 4,645, *T. furcata* colour 3,037, *T. javanica* colour 1,379, *T. alba* spot size 4,605, *T. furcata* spot size 3,029, *T. javanica* spot size 1,378.

Table S2, Figure S4). No variation in spot size according to hemisphere, latitude or their interaction emerges in the American (hemisphere by latitude interaction: $t = 1.72$; $p = 0.08$; Supporting Information Table S2, Figure S4) or Eastern barn owls (hemisphere by latitude interaction: $t = 1.49$; $p = 0.14$; Table 1; Supporting Information Table S2, Figure S4). Finally, in all lineages spot size is smaller in populations inhabiting islands than in those on the mainland (Table 1; Supporting Information Table S2).

3.2 | Variation in plumage traits according to climate

In all three lineages of the common barn owl group, we observed significant variation in breast plumage colour according to the annual rainfall recorded around the sites where specimens were collected (Table 2). In particular, the degree of melanin-based plumage darkness increases with increasing annual precipitation (Figure 3). In addition, in Western and American barn owls, plumage gets darker with decreasing mean annual temperature, but this is not the case for the Eastern barn owl lineage (Table 2; Figure 3). Conversely, temperature and rainfall do not predict the size of black spots in either *T. alba* or *T. furcata*, while in *T. javanica* the spot size decreases at increasing temperature (Table 2; Supporting Information Table S4). However, the latter pattern is not supported when the analysis was performed on the subsample of sexed individuals (Supporting Information Table S3). Finally, when data on *T. glaucops* were excluded, a negative relationship between spot size and rainfall emerges within the American barn owls (Supporting Information Table S4). The results which are not consistent in all the analyses should be taken with caution. All the other results are qualitatively similar in the analyses of the subsample of sexed individuals (Supporting Information Table S3) and in those excluding data on *T. glaucops*, *T. rosenbergii* and *T. nigrobrunnea* (Supporting Information Table S4).

No significant effect of the interaction between temperature and precipitation was found in any of the three evolutionary lineages for either plumage colour ($0.21 < t < 1.08$; $0.83 < p < 0.27$) or spot size ($0.02 < t < 0.82$; $0.41 < p < 0.93$).

Finally, the analyses performed on the pooled lineages confirm the effect of rainfall on plumage observed in the separate analyses (−0.166 ± 0.038, $t = 4.40$, $p < 0.001$), and also showed that plumage gets darker at decreasing temperature (0.101 ± 0.050, $t = 2.01$, $p = 0.044$). No significant effect of rainfall (−0.069 ± 0.119, $t = 0.58$, $p = 0.56$) or temperature (−0.124 ± 0.164, $t = 0.76$, $p = 0.45$) was detected on spot size.

4 | DISCUSSION

The main result of this study is that barn owls living in the Afro-Palaearctic region, in the Americas and in Australasia are consistently dark-coloured in areas characterized by intense annual rainfall

TABLE 2 Variation in plumage colour and spot size according to temperature and rainfall in the three lineages of the common barn owl group

	Plumage colour			Spot size		
	Coefficient (*SE*)	***t***	***p***	**Coefficient (*SE*)**	***t***	***p***
Western barn owl (*Tyto alba*)						
Intercept	6.840 (0.147)			25.384 (0.869)		
Island	**0.282 (0.118)**	**2.39**	**0.017**	**−2.047 (0.312)**	**6.55**	**<0.001**
Temperature	**0.174 (0.067)**	**2.60**	**0.009**	−0.208 (0.251)	0.83	0.41
Rainfall	**−0.140 (0.041)**	**3.39**	**<0.001**	−0.034 (0.147)	0.23	0.81
Other plumage trait	**−0.131 (0.004)**	**33.43**	**<0.0001**	**−1.471 (0.044)**	**33.17**	**<0.001**
American barn owl (*Tyto furcata*)						
Intercept	7.960 (0.170)			29.129 (0.619)		
Island	−0.291 (0.169)	1.72	0.08	**−1.985 (0.533)**	**3.72**	**<0.001**
Temperature	**0.145 (0.067)**	**2.16**	**0.031**	0.295 (0.218)	1.35	0.18
Rainfall	**−0.162 (0.061)**	**2.66**	**0.008**	**−0.321 (0.194)**	**1.66**	**0.10**
Other plumage trait	**−0.155 (0.006)**	**28.07**	**<0.001**	**−1.325 (0.047)**	27.95	**<0.001**
Eastern barn owl (*Tyto javanica*)						
Intercept	6.727 (0.385)			23.560 (0.884)		
Island	0.119 (0.184)	0.65	0.52	−1.574 (0.699)	2.25	0.024
Temperature	−0.003 (0.091)	0.03	0.98	**−0.756 (0.349)**	**2.17**	**0.030**
Rainfall	**−0.236 (0.084)**	**2.82**	**0.005**	0.003 (0.319)	0.01	0.99
Other plumage trait	**−0.040 (0.006)**	**6.63**	**<0.001**	**−0.789 (0.113)**	**6.99**	**<0.001**

Note. The effects of the interaction between temperature and rainfall are reported in the main text. Bold type indicates statistical significance. Residual degrees of freedom: *T. alba* 4,593, *T. furcata* 3,027, *T. javanica* 1,372.

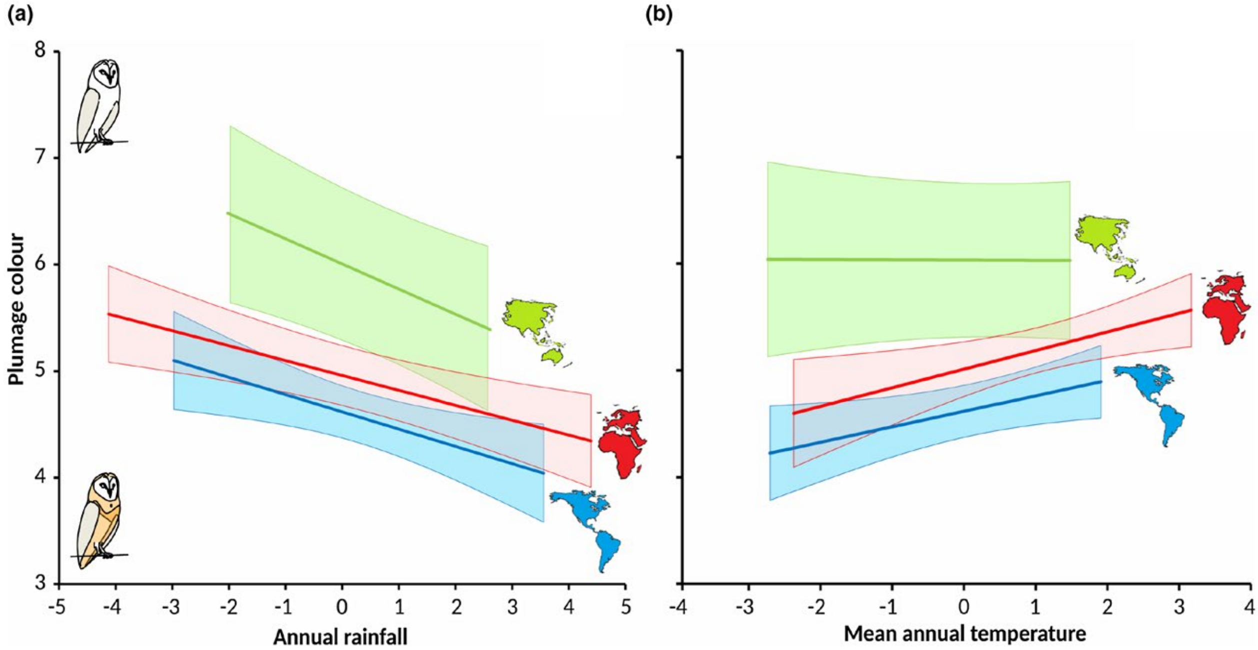


FIGURE 3 Relationship between rainfall and temperature and plumage colour (1 = dark red; 8 = white) in the three lineages of the common barn owl group. (a) Plumage colour according to annual rainfall; (b) plumage colour according to mean annual temperature. The Western barn owl *Tyto alba*: red line; the American barn owl *Tyto furcata*: blue line; the Eastern barn owl *Tyto javanica*: green line. Regression lines and 95% confidence intervals (coloured bands) are shown [from the generalized least squares (GLS) models reported in Table 2]. Values of annual rainfall and mean annual temperature were standardized within each taxon to facilitate comparison among the trends [Colour figure can be viewed at wileyonlinelibrary.com]

rather than in drier regions. This common pattern of variation in pheomelanin-based pigmentation was observed even though the geographical distribution of colour morphs in the three different lineages is heterogeneous (Figure 2). This finding is in line with the predicted variation in colour according to Gloger's rule (Gloger, 1833), postulating that dark-coloured animals should be more common in humid than in dry habitats, and provides the first support at the worldwide scale on a huge sample of individuals that local climate can drive phenotypic evolution and geographical polymorphism. The observation that a consistent association between plumage colour and rainfall is shared by three distinct lineages, separated by *c.a.* 3–4 million years of independent evolution (Uva et al., 2018), supports the hypothesis that natural selection promoted convergent evolution of plumage colour by favouring different morphs depending on the precipitation level. This interpretation is corroborated by the fact that expression of plumage colour is strongly genetically determined and heritable, as well as weakly sensitive to variation in individual condition (Roulin & Dijkstra, 2003; San-Jose et al., 2017). Therefore, different plumage colour might be selected under different rainfall conditions rather than be the result of climate affecting the expression of plumage traits.

Although Gloger's rule has been verified in a number of animal populations, spanning from insects (Mayr, 1963) to birds (Burtt & Ichida, 2004; Delhey, 2018; Zink & Remsen, 1986) and mammals (Kamilar & Bradley, 2011; Stoner et al., 2003), its proximate mechanisms are still unclear. The main hypothesis links colour polymorphism with camouflage: dark individuals can be favoured in humid habitats because their colouration is cryptic where low environmental light and dense vegetation are common (Delhey, 2018; Passarotto et al., 2018). In the case of a nocturnal predator, like the barn owl, individuals displaying a darker plumage of the ventral body side can be favoured in cloudy, rainy and vegetated environments because their prey cannot easily detect their shape against the dark sky (i.e., when the moon is covered by the clouds or by the tree canopies), as also suggested by preliminary results showing that darker individuals are more efficient in hunting when moonlight is low (our unpublished results). This prediction is partly fulfilled in our study system. Indeed, statistical models similar to those shown in Table 2 but including the mean annual cloud coverage or the vegetation structure (as a four-level category indicating increasing vegetation coverage) as predictor of plumage colour instead of temperature and rainfall, showed that Western and American barn owls living in environments with high levels of cloud coverage and more vegetation are significantly darker than in areas with fewer clouds or more open habitats, respectively (*T. alba* clouds: −0.184 ± 0.060, $t = 3.05$, $p = 0.003$; *T. alba* vegetation: −0.099 ± 0.048, $t = 2.05$, $p = 0.040$; *T. furcata* clouds: −0.197 ± 0.072, $t = 2.74$, $p = 0.006$; *T. furcata* vegetation: −0.141 ± 0.050, $t = 2.83$, $p = 0.005$). A similar, but non-significant, trend was observed in *T. javanica* (clouds: −0.095 ± 0.069, $t = 1.38$, $p = 0.17$; vegetation: −0.100 ± 0.052, $t = 1.92$, $p = 0.06$). The correlative nature of our data does not allow us to disentangle whether the darker plumage is favoured as a phenotypic adaptation to precipitation per se, or through the lighting condition of the environment, as suggested in other Strigiformes (Passarotto et al., 2018). In addition, previous evidence suggested that dark-plumaged barn owls develop feathers more resistant to wear (Roulin, Mangels, Wakamatsu, & Bachmann, 2013), possibly indicating that melanic plumage can be selected where sources of feather damage, like parasites in humid climates and/or rubbing wings against dense vegetation, are abundant (Burtt & Hichida, 2004; Goldstein et al., 2004; Ruiz-De-Castañeda, Burtt, Gonzalez-Braojos, & Moreno, 2012). Finally, more melanin-pigmented feathers have been also shown to repel water more efficiently than light-coloured feathers (Trullas, Terblanche, Blackburn, & Chown, 2008; Walsberg, Campbell, & King, 1978), and might thus be promoted in rainy environments to enhance body drying. We admit however that these interpretations are not conclusive and further experimental research is needed to better explain the proximate mechanism(s) underpinning the observed pattern of variation in plumage colour according to rainfall in these organisms.

In *T. alba* and *T. furcata*, but not in *T. javanica*, plumage colour is also darker in colder regions. Darker individuals seem therefore to be better able to cope in cold temperature or to be better adapted to environmental factors prevailing in cooler environments. This finding is coherent with Bogert's thermal melanism rule, predicting that dark individuals are advantaged under conditions of low temperature as they heat up faster than light individuals at a given level of solar radiation (Bogert, 1949; Trullas, Wyk, & Spotila, 2007; Trullas et al., 2008). Although this rule was conceived for ectothermic organisms, recent studies have provided evidence that it can also be applied to integuments of endothermic animals, like mammals (Caro, 2005; Nigenda-Morales et al., 2018) and birds (Delhey, 2018; Fargallo, Martínez, Wakamatsu, Serrano, & Blanco, 2018; Friedman & Remeš, 2016; Galvan et al., 2018). Our results add evidence at a very large spatial scale that local temperature can, at least partly, determine the body colouration in warm-blooded animals, as well as in organisms not continuously exposed to solar radiation, such as cavity-nesting and nocturnal species. Although we cannot exclude the possibility that a direct effect of solar radiation might help darker owls to increase their body temperature when they start to hunt just before sunset, thus potentially conferring a direct advantage compared to lighter ones, our findings suggest that the level of melanization might have some thermoregulation functions irrespective of the exposure to solar radiation. Melanization could help adaptation to cold climate directly (e.g., more melanic feathers might improve thermic insulation) or, considering that colouration is associated with several physiological functions, via a pleiotropic effect (Ducrest et al., 2008). Why this pattern was observed only in *T. alba* and *T. furcata* is a matter of speculation. A possibility is that in these two lineages dark colour was positively selected during the recolonization of high latitude regions after the last glaciation (Antoniazza, Burri, Fumagalli, Goudet, & Roulin, 2010; Antoniazza et al., 2014). This is especially the case for the Northern Hemisphere, where the Last Glacial Maximum was more pronounced. The thermal melanism hypothesis seems to explain the colour polymorphism observed in Europe, where the well-known latitudinal cline in plumage colour is considered an adaptation of different genotypes to local conditions along a temperature gradient (Antoniazza et al., 2010, 2014), and in North America, where an association between dark plumage and cold climate has already been detected (Roulin & Randin, 2015). On the other hand, *T. javanica* inhabits a smaller latitudinal range that is closer to the tropics, with less pronounced variation in ambient temperatures than in the range of distribution of the other two barn owl lineages (Figure 2), suggesting that there might be a threshold to observing an effect of temperature on the evolution of feather pigmentation.

A further consideration concerns the evidence that polymorphism in plumage colour depending on rainfall and temperature seem to be independent evolutionary processes. Indeed, a significant effect of the interaction between these climatic variables was not found in any of the barn owl lineages studied here. A similar pattern was recently shown in two studies of the Australian avifauna (Delhey, 2018; Friedman & Remeš, 2016), thus indicating that both rainfall and precipitation can concomitantly act as selective pressures that affect plumage colour traits. The combined effects of these climatic factors, which vary in space depending on latitude, elevation and distance from oceans, which in turn considerably differ among the ranges of distribution of the three barn owl lineages, can thus explain why Western, American and Eastern barn owls show different geographical distributions of their colour morphs (Table 1; Figure 2; Supporting Information Figure S3; see also Roulin et al., 2009; Roulin & Salamin, 2010).

Differently from plumage colour, spot size was not predicted by climate, with the only exception being temperature for *T. javanica*. Although these traits are partly genetically linked (Roulin & Jensen, 2015), this difference might be explained by the fact that black spots cover a small proportion of the plumage surface, thus limiting their scope to be involved in camouflage, feather resistance or body-drying functions, and because spottiness seems to be more involved in mate choice and sexual selection than plumage colouration (Antoniazza et al., 2010, 2014; Roulin & Ducrest, 2011; Roulin, Jungi, Pfister, & Dijkstra, 2000; Roulin et al., 2001). However, this result apparently contradicts previous studies at smaller scales reporting that individuals with larger spots are more abundant in colder regions (Roulin & Randin, 2015, 2016). We cannot exclude that spot size can help to thermoregulate, as suggested in *T. javanica*, but in the other two lineages such a possible function might have been masked in the present analyses because populations living in tropical and warmer habitats are more spotted than those at temperate latitudes, as indicated by the negative trend of spot size with latitude consistently observed in all the lineages (Table 1; Roulin et al., 2009). Thus, the possible contribution of spot size to thermoregulation may be more pronounced in colder areas and be detectable at spatial scales smaller than that used in this study.

An additional consistent pattern in melanin-based colouration among the three lineages was observed in spot size: irrespective of their plumage colour, populations living on islands display significantly smaller black spots than do mainland populations. This result is consistent with a previous study performed at the subspecies level and with a smaller sample size (Roulin & Salamin, 2010). A possibility is that a given level of pigmentation can be indirectly favoured on islands through the positive selection of individuals displaying some phenotypic traits that are adaptive in the process of island colonization and are genetically linked to colouration. This might be the case because in the barn owl melanin-based colour traits are known to be frequently associated with several physiological processes (Roulin & Ducrest, 2011), including the ability to resist various stressful factors (Almasi, Roulin, Jenni-Eiermann, & Jenni, 2008), which can be particularly important during island colonization.

In conclusion, we found strong evidence of convergent evolution of plumage colour compatible with the main biogeographical rules during three concomitant adaptive radiations of the common barn owl group. From a macroevolutionary perspective, the adaptation of single populations to local climate promoting geographical variation in traits linked to mate choice and sexual selection can favour a series of quick speciation events (van Doorn, Edelaar, & Weissing, 2009; Safran, Scordato, Symes, Rodríguez, & Mendelson, 2013), especially in species with limited dispersal capacity and with populations inhabiting distant and isolated areas. This might be the case for *T. rosenbergii*, *T. nigrobrunnea* and *T. glaucops*, which are morphologically and geographically distinct populations identified as independent species. An additional implication of these results is that melanin-based colouration is expected to change in response to anthropogenic climate change. Under the current scenario of a change in global climate, the frequency of light-coloured individuals is therefore expected to increase in regions where dry habitats are expanding and/or where annual temperature is increasing. On the other hand, the incidence of dark individuals should prevail in regions where humidity is predicted to increase. Melanin-based colour has therefore the potential to be used as a biomarker of current and future adaptation of wild organisms to climate change.

ACKNOWLEDGMENTS

We thank all of the curators who opened their museums for the measurement of barn owl skins, as well as for their hospitality. This study was financed by the Swiss National Science Foundation, the American Natural History Museum in New York, the Swiss Academy of Sciences, the Basler Stiftung fur biologische Forschung, the “Fondation du 450eme anniversaire”, and “Fondation Agassiz” of the University of Lausanne. We thank Roberto Ambrosini and Brian J. Smith for statistical advice.

AUTHOR CONTRIBUTIONS

A. Romano, A. Roulin conceived the study; A. Roulin collected the data; A. Romano, R. Séchaud, A. H. Hirzel performed the statistical analyses; A. Romano drafted the manuscript; all the authors contributed to the final version of the paper.

DATA ACCESSIBILITY

The dataset analysed during the current study is available from the corresponding author on request.

ORCID

Andrea Romano https://orcid.org/0000-0002-0945-6018

REFERENCES

Aliabadian, M., Alaei-Kakhki, N., Mirshamsi, O., Nijman, V., & Roulin, A. (2016). Phylogeny, biogeography, and diversification of barn owls (Aves: Strigiformes). *Biological Journal of the Linnean Society*, *119*, 904–918. https://doi.org/10.1111/bij.12824

Allen, J. A. (1877). The influence of physical conditions in the genesis of species. *Radical Reviews*, *1*, 108–140.

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. *Hormones and Behavior*, *54*, 217–223. https://doi.org/10.1016/j.yhbeh.2008.02.021

Antoniazza, S., Burri, R., Fumagalli, L., Goudet, J., & Roulin, A. (2010). Local adaptation maintains clinal variation in melanin-based coloration of European barn owls (*Tyto alba*). *Evolution*, *64*, 1944–1954.

Antoniazza, S., Ricardo, K., Neuenschwander, S., Burri, R., Gaigher, A., Roulin, A., & Goudet, J. (2014). Natural selection in a post-glacial range expansion: The case of the colour cline in the European barn owl. *Molecular Ecology*, *23*, 5508–5523. https://doi.org/10.1111/mec.12957

Barton, N. H. (2010). What role does natural selection play in speciation? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 1825–1840. https://doi.org/10.1098/rstb.2010.0001

Bergmann, K. G. L. C. (1847). Ueber die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse. *Gottinger Studien*, *3*, 595–708.

Bishop, T. R., Robertson, M. P., Gibb, H., Van Rensburg, B. J., Braschler, B., Chown, S. L., ... Parr, C. L. (2016). Ant assemblages have darker and larger members in cold environments. *Global Ecology and Biogeography*, *25*, 1489–1499. https://doi.org/10.1111/geb.12516

Bogert, C. M. (1949). Thermoregulation in reptiles, a factor in evolution. *Evolution*, *3*, 195–211. https://doi.org/10.1111/j.1558-5646.1949.tb00021.x

Brandt, T., & Seebass, C. (1994). *The Barn Owl: Ecology of mysterious cultural successor.* Wiesbaden, Germany: Aula, Verlag.

Burtt, E. H., & Ichida, J. M. (2004). Gloger’s rule, feather-degrading bacteria, and color variation among song sparrows. *The Condor*, *106*, 681–686. https://doi.org/10.1650/7383

Caro, T. (2005). The adaptive significance of coloration in mammals. *BioScience*, *55*, 125–136. https://doi.org/10.1641/0006-3568(2005)055[0125:TASOCI]2.0.CO;2

Cayford, J. (1992). Barn owl ecology on East Anglian farmland. *RSPB Conservation Reviews*, *6*, 45–50.

Colvin, B. A. (1985). Common Barn-Owl population decline in Ohio and the relationship to agricultural trends. *Journal of Field Ornithology*, *56*, 224–235.

Cuthill, I. C., Allen, W. L., Arbuckle, K., Caspers, B., Chaplin, G., Hauber, M. E. ,. ... Caro, T. (2017). The biology of color. *Science*, *357*, 470. https://doi.org/10.1126/science.aan0221

Delhey, K. (2017). Gloger’s rule. *Current Biology*, *27*, R689–R691. https://doi.org/10.1016/j.cub.2017.04.031

Delhey, K. (2018). Darker where cold and wet: Australian birds follow their own version of Gloger’s rule. *Ecography*, *41*, 673–683. https://doi.org/10.1111/ecog.03040

Dreiss, A., & 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. https://doi.org/10.1111/j.1095-8312.2010.01503.x

Ducrest, A.-L., Keller, L., & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends* *in Ecology and Evolution*, *23*, 502–510. https://doi.org/10.1016/j.tree.2008.06.001

Fargallo, J. A., Martínez, F., Wakamatsu, K., Serrano, D., & Blanco, G. (2018). Sex-dependent expression and fitness consequences of sunlight-derived color phenotypes. *American Naturalist*, *191*, 726–743.

Friedman, N. R., & Remeš, V. (2016). Ecogeographic gradients in plumage coloration among Australasian songbird clades. *Global Ecology and Biogeography*, *26*, 261–274.

Galvan, I., Rodríguez-Martínez, S., & Carrascal, L. M. (2018). Dark pigmentation limits thermal niche position in birds. *Functional Ecology*, *32*, 1531–1540.

Gloger, C. L. (1833). *Das Abandern der Vogel durch Einfluss des Klimas*. Breslau: August Schulz.

Goldstein, G., Flory, K. R., Browne, B. A., Majid, S., Ichida, J. M., & Burtt, E. H. Jr. (2004). Bacterial degradation of black and white feathers. *The Auk*, *121*, 656–659. https://doi.org/10.1642/0004-8038(2004)121[0656:BDOBAW]2.0.CO;2

Hill, G. E., & McGraw, K. J. (2006). *Bird coloration: Mechanisms and measurements* (Vol. *1*). Cambridge, MA: Harvard University Press.

Huey, R. B., Gilchrist, G. W., Carlson, M. L., Berrigan, D., & Serra, L. (2000). Rapid evolution of a geographic cline in size in an introduced fly. *Science*, *287*, 308–309. https://doi.org/10.1126/science.287.5451.308

Kamilar, J. M., & Bradley, B. J. (2011). Interspecific variation in primate coat colour supports Gloger's rule. *Journal of Biogeography*, *38*, 2270–2277. https://doi.org/10.1111/j.1365-2699.2011.02587.x

König, C., & Weick, W. (2008). *Owls. A guide to the owls of the world* (2nd ed.). London, UK: Christopher Helm.

Mayr, E. (1963). *Animal species and evolution*. Cambridge, MA: Harvard University Press.

Nigenda-Morales, S. F., Harrigan, R. J., & Wayne, R. K. (2018). Playing by the rules? Phenotypic adaptation to temperate environments in an American marsupial. *PeerJ*, *6*, e4512. https://doi.org/10.7717/peerj.4512

Passarotto, A., Parejo, D., Penteriani, V., & Avilés, J. M. (2018). Colour polymorphism in owls is linked to light variability. *Oecologia*, *187*, 61–73.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2014). *Nlme: Linear and nonlinear mixed effects models*. R package version 3.

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Roulin, A. (2003). Geographic variation in sexually selected traits: A role for direct selection or genetic correlation? *Journal of Avian Biology*, *34*, 251–258.

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

Roulin, A., Dijkstra, C., Riols, C., & Ducrest, A.-L. (2001). Female-and male-specific signals of quality in the barn owl. *Journal of Evolutionary Biology*, *14*, 255–266. https://doi.org/10.1046/j.1420-9101.2001.00274.x

Roulin, A., & Ducrest, A.-L. (2011). Association between melanism, physiology and behaviour: A role for the melanocortin system. *European Journal of Pharmacology*, *660*, 226–233. https://doi.org/10.1016/j.ejphar.2011.01.036

Roulin, A., & Jensen, H. (2015). Sex-linked inheritance, genetic correlations and sexual dimorphism in three melanin-based color traits in the barn owl. *Journal of Evolutionary Biology*, *28*, 655–666.

Roulin, A., Jungi, T. W., Pfister, H., & Dijkstra, C. (2000). Female barn owls (*Tyto alba*) advertise good genes. *Proceedings of the Royal Society B: Biological Sciences*, *267*, 937–941. https://doi.org/10.1098/rspb.2000.1093

Roulin, A., Mangels, J., Wakamatsu, K., & Bachmann, T. (2013). Sexually dimorphic melanin-based colour polymorphism, feather melanin content, and wing feather structure in the barn owl (*Tyto alba*). *Biological Journal of the Linnean Society*, *109*, 562–573.

Roulin, A., & Randin, C. F. (2015). Gloger's rule in North American barn owls. *The Auk*, *132*, 321–332. https://doi.org/10.1642/AUK-14-167.1

Roulin, A., & Randin, C. F. (2016). Barn owls display larger black feather spots in cooler regions of the British Isles. *Biological Journal of the Linnean Society*, *119*, 445–454. https://doi.org/10.1111/bij.12814

Roulin, A., & Salamin, N. (2010). Insularity and the evolution of melanism, sexual dichromatism and body size in the worldwide-distributed barn owl. *Journal of Evolutionary Biology*, *23*, 925–934. https://doi.org/10.1111/j.1420-9101.2010.01961.x

Roulin, A., Uva, V., & Romano, A. (2018). A melanin-based trait is more strongly related to body size in the tropics than in temperate regions in the globally distributed barn owl family. *Journal of Evolutionary Biology*, *31*, 1932–1944.

Roulin, A., Wink, M., & Salamin, N. (2009). Selection on a eumelanic ornament is stronger in the tropics than in temperate zones in the worldwide-distributed barn owl. *Journal of Evolutionary Biology*, *22*, 345–354. https://doi.org/10.1111/j.1420-9101.2008.01651.x

Ruiz-De-Castañeda, R., Burtt, E. H., Gonzalez-Braojos, S., & Moreno, J. (2012). Bacterial degradability of an intrafeather unmelanized ornament: A role of feather-degrading bacteria in sexual selection? *Biological Journal of the Linnean Society*, *105*, 409–419.

Safran, R. J., Scordato, E. S., Symes, L. B., Rodríguez, R. L., & Mendelson, T. C. (2013). Contributions of natural and sexual selection to the evolution of premating reproductive isolation: A research agenda. *Trends in Ecology and Evolution*, *28*, 643–650. https://doi.org/10.1016/j.tree.2013.08.004

San-Jose, L. M., Ducrest, A. L., Ducret, V., Simon, C., Richter, H., Wakamatsu, K., & Roulin, A. (2017). MC1R variants affect the expression of melanocortin and melanogenic genes and the association between melanocortin genes and coloration. *Molecular Ecology*, *26*, 259–276.

Smith, B. J., Yan, J., & Cowles, M. K. (2008). Unified Geostatistical Modeling for Data Fusion and Spatial Heteroskedasticity with R Package ramps. *Journal of Statistical Software*, *25*, 1–21.

Souza, D. P., Asfora, P. H., Lira, T. C., & Astúa, D. (2010). Small mammals in Barn Owl (*Tyto alba*–Aves, Strigiformes) pellets from northeastern Brazil, with new records of *Gracilinanus* and *Cryptonanus* (Didelphimorphia, Didelphidae). *Mammalian Biology*, *75*, 370–374. https://doi.org/10.1016/j.mambio.2009.08.003

Stoner, C. J., Caro, T. M., & Graham, C. M. (2003). Ecological and behavioral correlates of coloration in artiodactyls: Systematic analyses of conventional hypotheses. *Behavioral Ecology*, *14*, 823–840. https://doi.org/10.1093/beheco/arg072

Trullas, C. S., Terblanche, J. S., Blackburn, T. M., & Chown, S. L. (2008). Testing the thermal melanism hypothesis: A macrophysiological approach. *Functional Ecology*, *22*, 232–238. https://doi.org/10.1111/j.1365-2435.2007.01377.x

Trullas, S. C., van Wyk, J. K., & Spotila, J. R. (2007). Thermal melanism in ectotherms. *Journal of Thermal Biology*, *32*, 235–245. https://doi.org/10.1016/j.jtherbio.2007.01.013

Uva, V., Päckert, M., Cibois, A., Fumagalli, L., & Roulin, A. (2018). Comprehensive molecular phylogeny of barn-owls and relatives (Family: Tytonidae). *Molecular Phylogenetics and Evolution*, *125*, 127–137.

van Doorn, G. S., Edelaar, P., & Weissing, F. J. (2009). On the origin of species by natural and sexual selection. *Science*, *326*, 1704–1707. https://doi.org/10.1126/science.1181661

Walsberg, G. E., Campbell, G. S., & King, J. R. (1978). Animal coat color and radiative heat gain: A re-evaluation. *Journal of Comparative Physiology*, *126*, 211–222. https://doi.org/10.1007/BF00688930

Wink, M., El-Sayed, A.-A., Sauer-Gürth, H., & Gonzalez, J. (2009). Molecular phylogeny of owls (Strigiformes) inferred from DNA sequences of the mitochondrial cytochrome *b* and the nuclear *RAG-1* gene. *Ardea*, *97*, 581–591. https://doi.org/10.5253/078.097.0425

Zink, R. M., & Remsen, J. V. (1986). Evolutionary processes and patterns of geographic variation in birds. *Current Ornithology*, *4*, 1–69.

Züur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology with R. Statistics for biology and health*. New York, NY: Springer.

BIOSKETCH

The main goal of the research group lead by **Prof. Alexandre Roulin** is to understand the role of natural and sexual selection in the evolution and maintenance of genetic and phenotypic variation in melanin-based colour traits by combining the disciplines of evolutionary ecology, biogeography, behavioural ecology, genetics, population genetics and even biomedicine. The specific aims of our research are to determine the adaptive function of alternative melanin-based colour traits and to identify how ecological, social and physiological factors influence and maintain inter-individual variation in melanin-based colouration and other associated phenotypic traits, as well as disclose the mechanisms underlying differences in melanocortin levels between differently coloured individuals.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Romano A, Séchaud R, Hirzel AH, Roulin A. Climate-driven convergent evolution of plumage colour in a cosmopolitan bird. *Global Ecol Biogeogr.* 2019;28:496–507. https://doi.org/10.1111/geb.12870

Climate-driven convergent evolution of plumage colour in a cosmopolitan species

Andrea Romano, Robin Séchaud, Alexandre H. Hirzel, Alexandre Roulin

Supporting Information

Table S1. Comparison between the Akaike's information criterion (AIC) of the models reported in Table 1 and Table 2 excluding or including spatial autocorrelation.

Model	$\mathrm{AIC}_{\text{(without spatial autocorrelation)}}$	$\mathrm{AIC}_{\text{(with spatial autocorrelation)}}$	ΔAIC
Plumage colour			
Geographical variation in *T. alba*	18715.98	16859.49	1856.49
Geographical variation in *T. furcata*	12766.46	12448.2	318.26
Geographical variation in *T. javanica*	4684.323	4243.110	441.213
Climatic variation in *T. alba*	16664.44	15698.52	965.92
Climatic variation in *T. furcata*	11918.51	11739.22	179.29
Climatic variation in *T. javanica*	4908.95	4203.068	705.882
Spot size			
Geographical variation in *T. alba*	29225.15	27838.84	1386.31
Geographical variation in *T. furcata*	19218.35	18934.06	284.29
Geographical variation in *T. javanica*	8667.988	8312.139	355.849
Climatic variation in *T. alba*	28569.27	26866.38	1702.89
Climatic variation in *T. furcata*	18402.93	18243.08	159.85
Climatic variation in *T. javanica*	8467.635	8247.721	219.914

Table S2. Geographic variation in plumage colour and spot size in the three lineages of the common barn owl in the subsample including only individuals for which the sex was known. The coefficients of all the main terms (hemisphere, latitude, island, sex) refer to models excluding the hemisphere by latitude interaction. The effect of hemisphere by latitude interaction refers to models including this term in addition to all the main predictors. Details of the variation in plumage traits according to latitude in the two hemispheres are provided in the text and in Figure. S3-S4.

	Plumage colour			*Spot size*		
	Coefficient (SE)	t	P	Coefficient (SE)	t	P
*Western barn owl (*Tyto alba*)*						
Intercept	6.824 (0.566)			8.456 (1.802)		
Sex	**-0.953 (0.045)**	**21.14**	**<0.001**	**3.241 (0.150)**	**21.71**	**<0.001**
Island	**0.536 (0.146)**	**3.68**	**<0.001**	**-2.960 (0.477)**	**6.20**	**<0.001**
Absolute latitude	-0.003 (0.010)	0.30	0.77	**-0.130 (0.031)**	**4.24**	**<0.001**
Hemisphere	**-0.490 (0.309)**	**1.59**	**0.12**	**5.922 (0.981)**	**6.04**	**<0.001**
Hemisphere × Absolute latitude		0.87	0.38		**4.15**	**<0.001**
*American barn owl (*Tyto furcata*)*						
Intercept	7.311 (0.512)			17.279 (1.966)		
Sex	**-1.949 (0.062)**	**31.49**	**<0.001**	**4.646 (0.193)**	**24.02**	**<0.001**
Island	0.080 (0.197)	0.41	0.68	**-1.937 (0.619)**	**3.13**	**0.002**
Absolute latitude	0.009 (0.009)	0.95	0.34	-0.032 (0.038)	0.85	0.39
Hemisphere	0.114 (0.267)	0.41	0.68	-1.765 (0.998)	1.77	0.07
Hemisphere × Absolute latitude		1.26	0.21		1.71	0.09
*Eastern barn owl (*Tyto javanica*)*						
Intercept	5.391 (0.733)			16.939 (2.404)		
Sex	**-0.565 (0.064)**	**8.77**	**<0.0001**	**3.197 (0.284)**	**11.25**	**<0.001**
Island	0.133 (0.197)	0.68	0.50	**-1.891 (0.862)**	**2.19**	**0.028**
Absolute latitude	**0.048 (0.021)**	**2.31**	**0.021**	-0.084 (0.063)	1.34	0.18
Hemisphere	0.351 (0.354)	0.965	0.33	-0.862 (1.286)	0.67	0.50
Hemisphere × Absolute latitude		**3.76**	**0.0002**		1.24	0.21

Residual degrees of freedom: *T. alba* colour = 3708, *T. furcata* colour = 2614, *T. javanica* colour = 1082, *T. alba* spot size = 3688, *T. furcata* spot size = 2614, *T. javanica* spot size = 1081

Table S3. Variation in plumage colour and spot size in the three lineages of the common barn owl according to rainfall and temperature in the subsample including only individuals for which the sex was known.

	Plumage colour			*Spot size*		
	Coefficient (SE)	t	P	Coefficient (SE)	t	P
*Western barn owl (*Tyto alba*)*						
Intercept	7.465 (0.181)			22.290 (0.968)		
Sex	**-0.588 (0.045)**	**13.15**	**<0.001**	**2.026 (0.148)**	**13.69**	**<0.001**
Island	**0.283 (0.112)**	**2.53**	**0.014**	**-3.123 (0.316)**	**9.89**	**<0.001**
Temperature	**0.173 (0.075)**	**2.30**	**0.021**	**-0.496 (0.267)**	**1.85**	**0.06**
Rainfall	**-0.144 (0.044)**	**3.31**	**<0.001**	-0.176 (0.151)	1.17	0.24
Other plumage trait	**-0.115 (0.005)**	**25.32**	**<0.001**	**-1.280 (0.050)**	**25.65**	**<0.001**
*American barn owl (*Tyto furcata*)*						
Intercept	9.027 (0.214)			21.633 (0.767)		
Sex	**-1.486 (0.065)**	**22.70**	**<0.0001**	**2.731 (0.216)**	**12.64**	**<0.001**
Island	-0.029 (0.177)	0.16	0.87	**-1.661 (0.572)**	**2.90**	**0.004**
Temperature	0.136 (0.071)	1.92	0.055	0.034 (0.228)	0.15	0.88
Rainfall	**-0.134 (0.062)**	**2.17**	**0.029**	-0.248 (0.199)	1.25	0.21
Other plumage trait	**-0.102 (0.006)**	**17.08**	**<0.001**	**-0.984 (0.058)**	**17.00**	**<0.001**
*Eastern barn owl (*Tyto javanica*)*						
Intercept	7.249 (0.419)			17.333 (1.162)		
Sex	**-0.474 (0.069)**	**6.90**	**<0.001**	**2.933 (0.294)**	**9.96**	**<0.001**
Island	0.151 (0.181)	0.84	0.40	**-1.773 (0.742)**	**2.39**	**0.017**
Temperature	0.148 (0.102)	1.45	0.15	-0.589 (0.400)	1.48	0.14
Rainfall	**-0.268 (0.090)**	**2.98**	**0.003**	0.396 (0.357)	1.11	0.27
Other plumage trait	**-0.028 (0.009)**	**6.90**	**<0.001**	**-0.475 (0.129)**	**9.96**	**<0.001**

Residual degrees of freedom: *Tyto alba* = 3678, *Tyto furcata* = 2606, *Tyto javanica* = 1078

Table S4. Variation in plumage colour and spot size in the two lineages of the common barn owl group according to rainfall and temperature in the subsample excluding specimens of the insular taxa *T. glaucops* (in the main analyses considered within *T. furcata*), *T. nigrobrunnea* and *T. rosenbergii* (in the main analyses considered within *T. javanica*).

	Plumage colour			*Spot size*		
	Coefficient (SE)	t	P	Coefficient (SE)	t	P
*American barn owl (*Tyto furcata*)*						
Intercept	8.084 (0.150)			27.226 (0.597)		
Island	-0.058 (0.158)	0.37	0.71	**-2.222 (0.532)**	**4.18**	**<0.001**
Temperature	**0.126 (0.059)**	**2.12**	**0.034**	0.230 (0.212)	1.09	0.28
Rainfall	**-0.146 (0.056)**	**2.62**	**0.009**	**-0.415 (0.192)**	**2.16**	**0.031**
Other plumage trait	**-0.157 (0.006)**	**27.96**	**<0.001**	**-1,331 (0.048)**	**27.65**	**<0.001**
*Eastern barn owl (*Tyto javanica*)*						
Intercept	6.836 (0.387)			22.761 (0.868)		
Island	0.078 (0.183)	0.40	0.69	**-1.995 (0.666)**	**2.99**	**0.003**
Temperature	0.043 (0.096)	0.45	0.65	**-0.778 (0.339)**	**2.29**	**0.021**
Rainfall	**-0.221 (0.085)**	**2.61**	**0.009**	-0.138 (0.305)	0.45	0.65
Other plumage trait	**-0.037 (0.006)**	**5.86**	**<0.001**	**-0.690 (0.114)**	**6.04**	**<0.001**

Residual degrees of freedom: *Tyto furcata* 2919, *Tyto javanica* 1315

Table S5. Same model (variation in plumage colour according to climatic variable in *T. javanica*) assuming an increasing level of spatial autocorrelation. Results are consistent among the models.

		Coefficient (SE)	t	P
Range 1600 km				
	Intercept	6.727 (0.385)		
	Island	0.119 (0.184)	0.65	0.52
	Temperature	-0.003 (0.091)	0.29	0.98
	Rainfall	**-0.236 (0.084)**	**2.82**	**0.005**
	Other plumage trait	**-0.040 (0.006)**	**6.63**	**<0.001**
Range 2000 km				
	Intercept	6.765 (0.433)		
	Island	0.138 (0.175)	0.79	0.43
	Temperature	0.030 (0.090)	0.36	0.71
	Rainfall	**-0.237 (0.080)**	**2.94**	**0.003**
	Other plumage trait	**-0.042 (0.006)**	**7.01**	**<0.001**

Fig. S1. Recovery sites of all the specimens included in the analyses. *Tyto alba*: red points; *Tyto furcata*: blue points; *Tyto javanica*: green points.

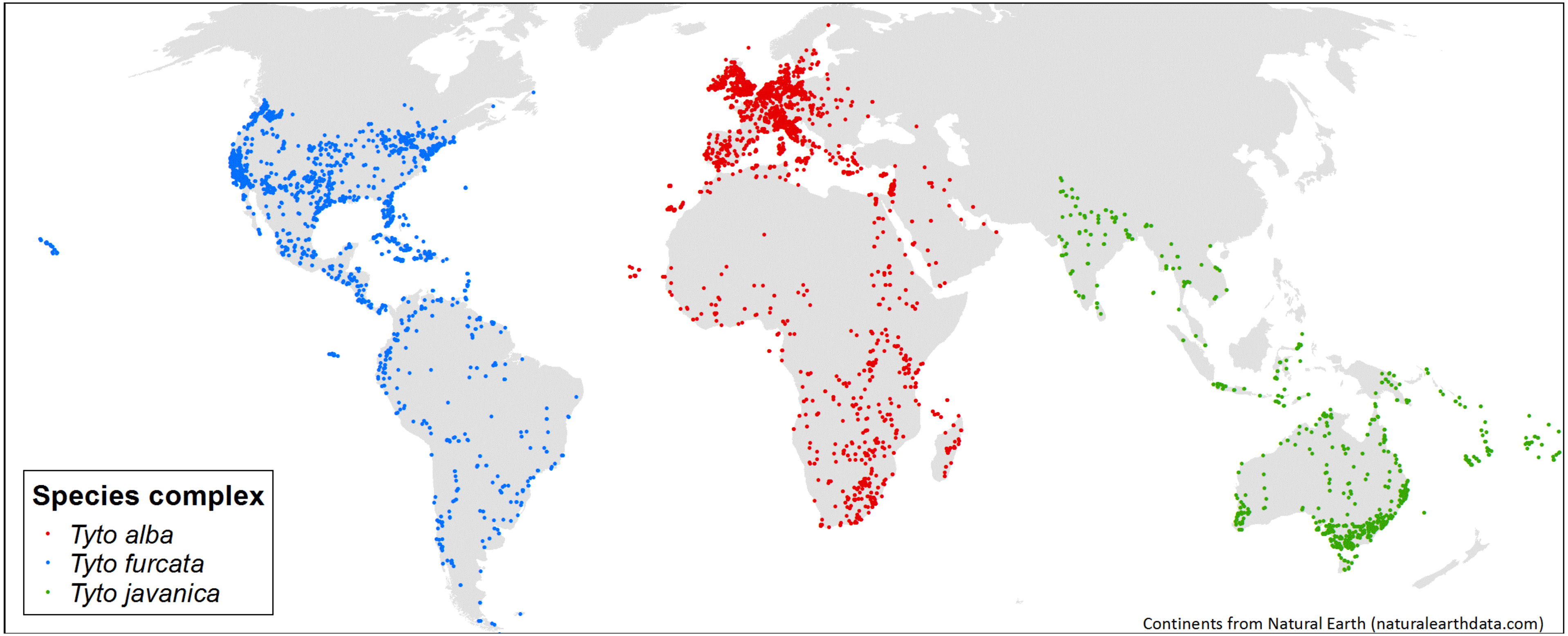


Fig. S2. Variograms of the final models reported in Table 1 and 2. Variograms of the final models reported in Table 1 and 2 showing that spatial dependence between datapoints has been successfully removed. Geographic variation in colour in *T. alba* (a); *T. furcata* (b); *T. javanica* (c). Geographic variation in spot size in *T. alba* (d); *T. furcata* (e); *T. javanica* (f). Variation in plumage colour according to climate in *T. alba* (g); *T. furcata* (h); *T. javanica* (i). Variation in spot size according to climate in *T. alba* (j); *T. furcata* (k); *T. javanica* (l). Distance is expressed in km.

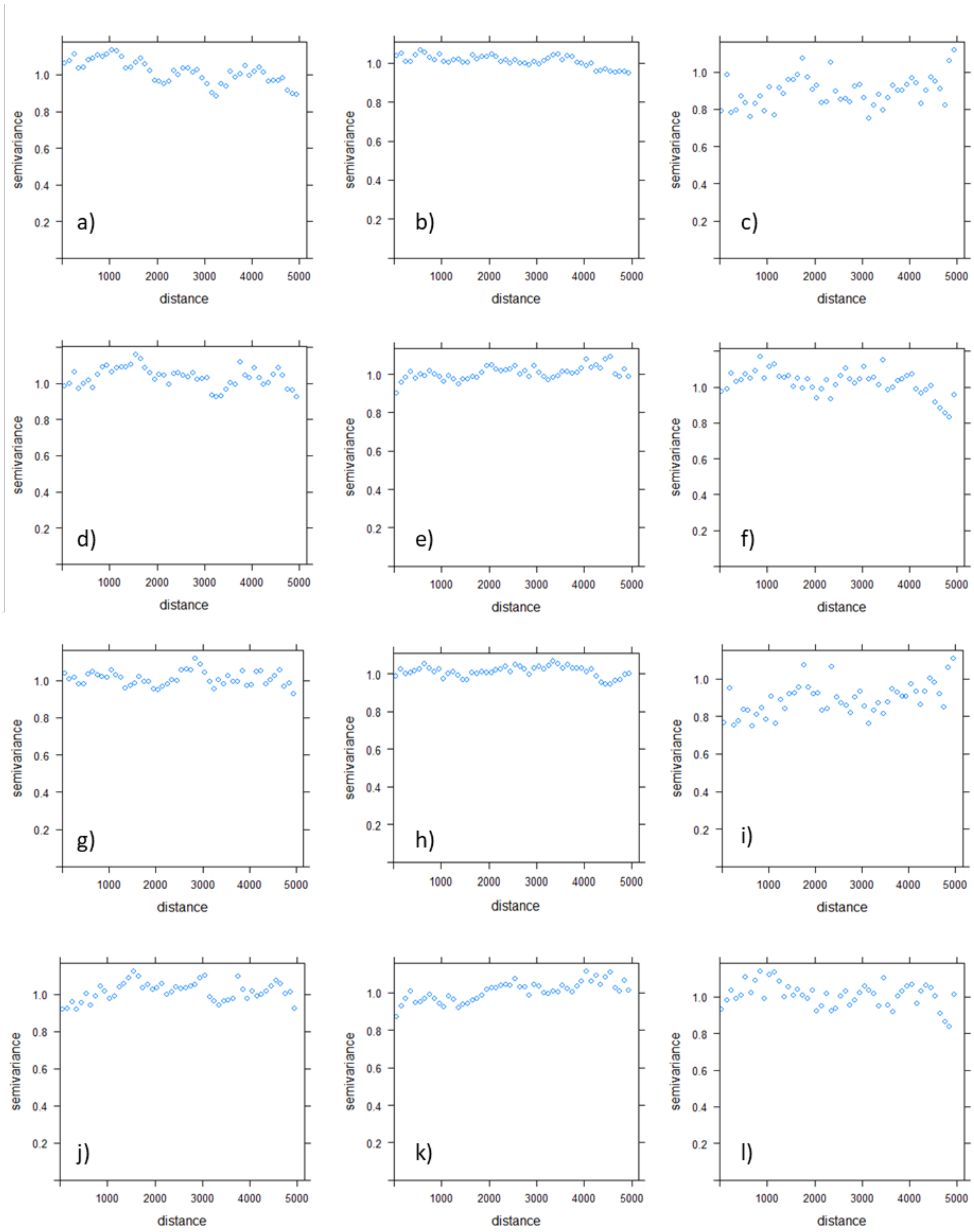


Fig. S3. Latitudinal variation in plumage colour in the two hemispheres in the three lineages of the barn owl. Latitudinal variation in plumage colour (1 = dark red; 8 = white) in the two hemispheres in the three lineages of the barn owl group. Regression lines and 95% confidence intervals are shown (from the GLS models reported in Table 1).

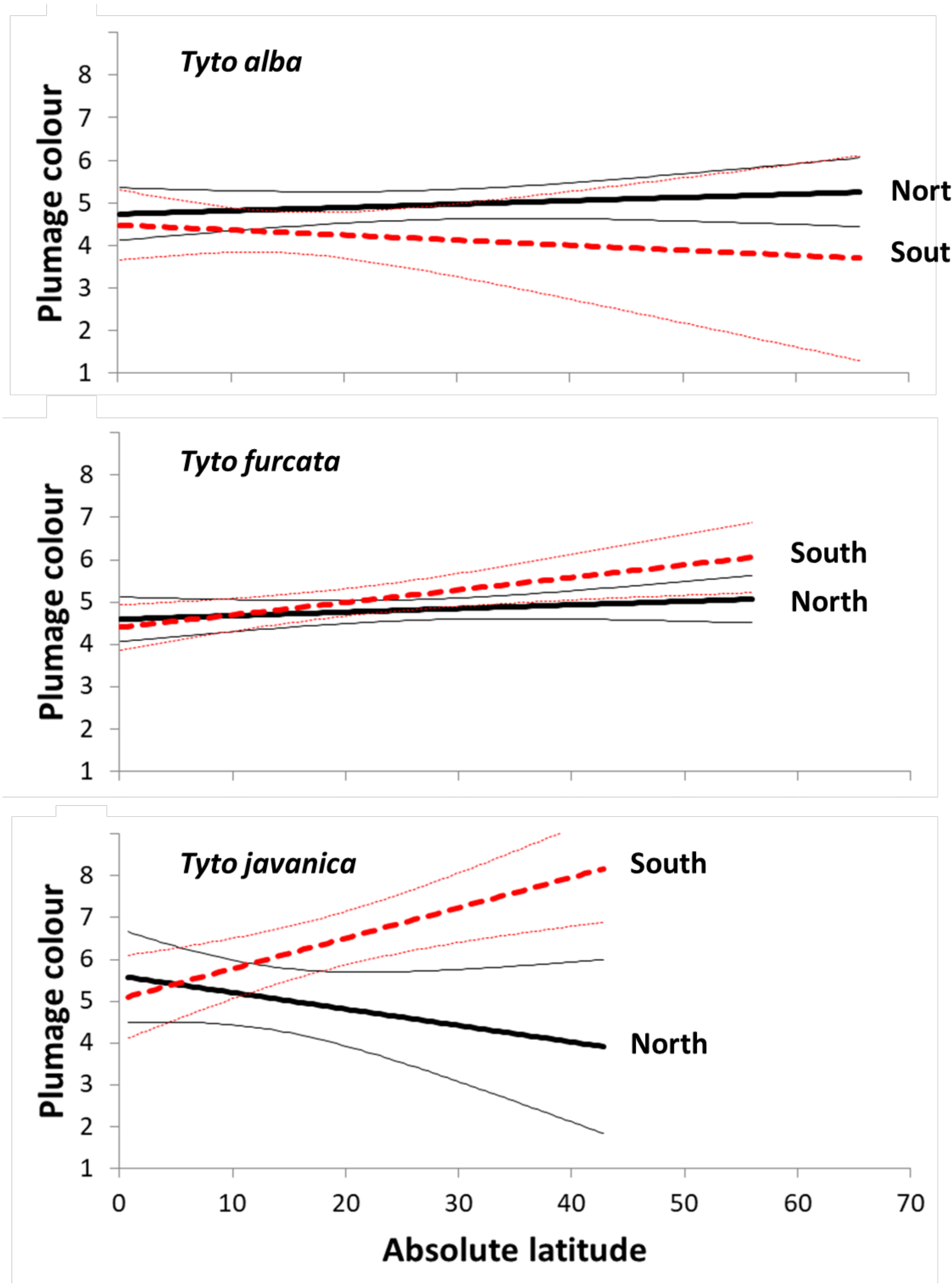
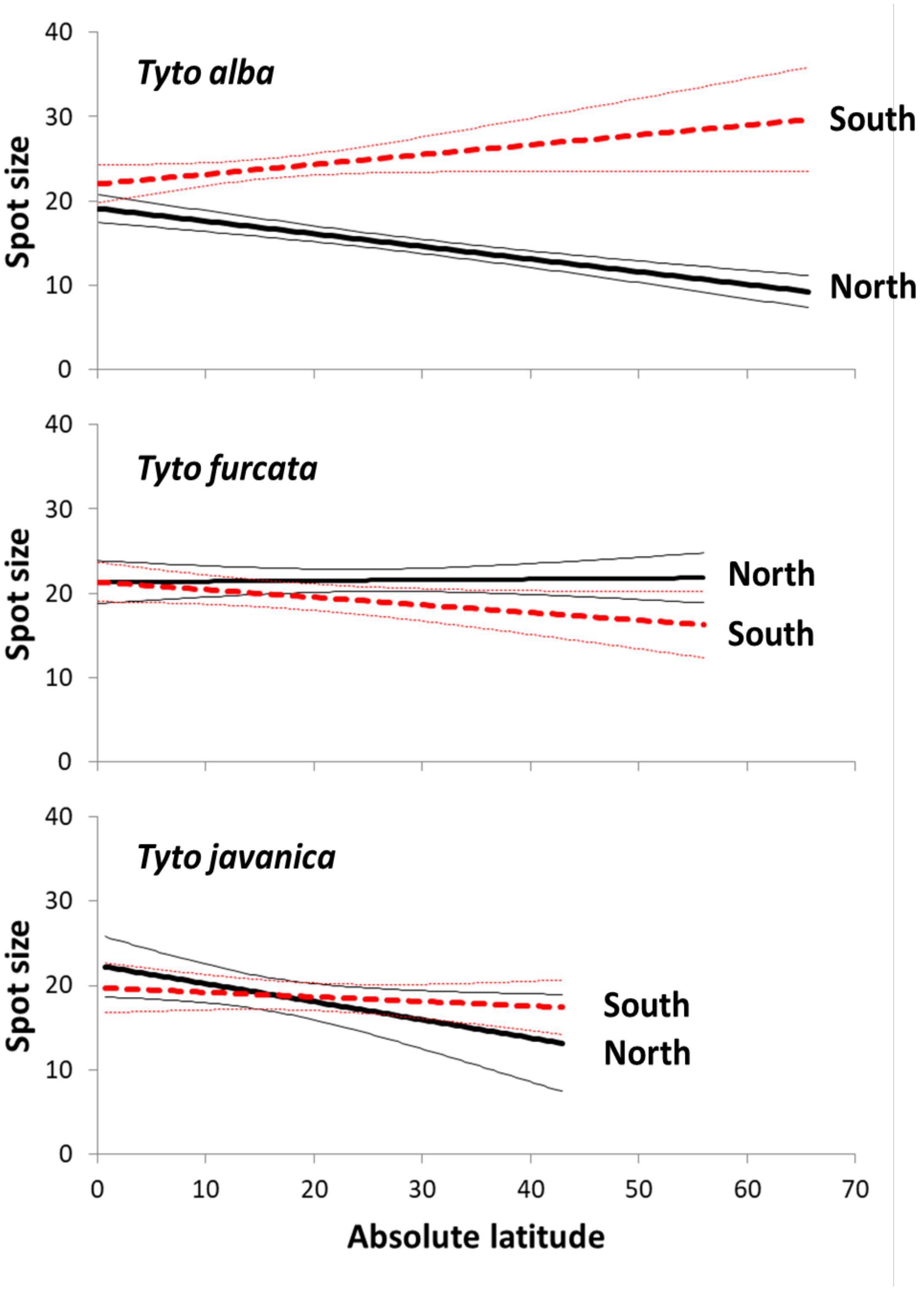


Fig. S4. Latitudinal variation in spot size in the two hemispheres in the three lineages of the barn owl. Latitudinal variation in spot size (expressed in mm) in the two hemispheres in the three lineages of the barn owl group. Regression lines and 95% confidence intervals are shown (from the GLS models reported in Table 1).



Appendix. Number of specimens of *Tyto alba*, *T. furcata* and *T. javanica* measured in each of 141 natural history museums (plus specimens collected by private citizens).

Country (State)	**City**	**Museum**	***Tyto alba***	***Tyto furcata***	***Tyto javanica***	**Total**
Australia	Adelaïde	South Australian Museum	2	2	114	118
Australia	Brisbane	Queensland Museum			51	51
Australia	Canberra	CSIRO Ecoystem Sciences			75	75
Australia	Darwin	Museum and Art Gallery of the Northern Territory			13	13
Australia	Melbourne	Museum Victoria	4	3	165	172
Australia	Perth	Western Australian Museum			54	54
Australia	Sydney	Australian Museum		1	110	111
Austria	Wien	Naturhistorisches Museum Wien	55	22	7	84
Belgium	Bruxelles	Royal Belgian Institute of Natural Sciences	118	5	4	127
Belgium	Tervuren	Royal Museum for Central Africa	110			110
Canada (Ontario)	Ottawa	Musée canadien de la Nature	6	12		18
Canada (Ontario)	Toronto	Royal Ontario Museum	21	54	4	79
Czech Republic	Prague	Narodni Muzeum	18	1		19
Denmark	Copenhagen	Natural History Museum of Denmark	58	7	8	73
Finland	Helsinki	Finnish Museum of Natural History	12			13
France	Lyon	Musée des Confluences	30	1	1	32
France	Nantes	Musée d'Histoire Naturelle de Nantes	26			26
France	Paris	Musée national d'Histoire Naturelle	141	20	12	173
Germany	Berlin	Museum für Naturkunde	80	6	21	107
Germany	Bonn	Alexander Koenig Research Museum	145	4	13	162
Germany	Braunschweig	Staatliches Naturhistorisches Museum Braunschweig	15	1	4	20
Germany	Bremen	Ubersee-Museum	29	2	3	34
Germany	Dresden	Senckenberg Natural History Museum	96	8	8	112
Germany	Frankfuhrt	Senckenberg Naturmuseum Frankfurt	58	9	1	68
Germany	Görlitz	Senckenberg Museum of Natural History Görlitz	14	2	1	17
Germany	Halberstadt	Museum Heineanum	85	3	2	90
Germany	Halle	Natural History Museum	13	5		18
Germany	Hamburg	Biozentrum Grindel und Zoologisches Museum	40		6	46

Germany	Kassel	Museum of Natural History in the Ottoneum	37			37
Germany	Munchen	Zoologisches Staatssammlung München	32	12	6	50
Germany	Wilhelmshaven	Institut für Vogelforschung	21			21
Great Britain (England)	Bristol	Bristol Museum and Art Gallery	24			24
Great Britain (England)	Cambridge	University Museum of Zoology	18	8	2	28
Great Britain (England)	Sevenoaks	Harrisson Institute	65	1	1	67
Great Britain (England)	Liverpool	World Museum Liverpool	33	4	13	50
Great Britain (England)	Manchester	Manchester Museum	14	2	1	17
Great Britain (England)	Newcastle	Great North Museum	44		3	47
Great Britain (England)	Tring	Natural History Museum at Tring	331	130	182	643
Great Britain (Scotland)	Edinburgh	National Museums of Scotland, Royal Museum	80	1	7	88
Great Britain (Scotland)	Glasgow	Natural History Museum	11			11
Great Britain (Scotland)	Invernes	Inverness Museum and Art Gallery	4			4
Great Britain (Scotland)	Perth	Perth Museum and Art Gallery	3			3
Great Britain (Wales)	Cardiff	National Museum Cardiff	21			21
Greece (Crete)	Heraklion	Natural History Museum of Crete	68			68
Ireland	Dublin	National Museum of Ireland	44	2	2	48
Israel	Tel Aviv	National Museum of Natural History at Tel-Aviv University	56			56
Italy	Bergamo	Museo di Scienze Naturali Enrico Caffi	13			13
Italy	Bologna	Italian National Ringing Centre	117			117
Italy	Brescia	Museo di Storia Naturale	12			12
Italy	Carmagnola	Museo di Storia Naturale	16			16
Italy	Faenza	Museo di Storia Naturale	7			7
Italy	Florence	Museo di Storia Naturale di Firenze	43	3	1	47
Italy	Forli	Museo Ornitologico Ferrante Foschi	9			9
Italy	Genoa	Museo di Storia Naturale	62			62
Italy	Milano	Museo Civico di Storia Naturale d Milano	89			89
Italy	Naples	Museo Zoologico di Napoli	2			2
Italy	Rome	Museo Civico di Zoologia di Roma	55			55
Italy	Terrasini	Terrasini Museum	32			32
Japan	Hyogo	National Museum of Nature and Science	3	1		4
Japan	Tsukuba	Geological Museum	1			1
Japan	Abiko	Yamashina Institute for Ornithology	5			5

Kenya	Nairobi	Nairobi National Museum	32			32
Netherland	Amsterdam	Zoological Museum	168	28	10	206
Netherland	Leiden	National Museum of Natural History	197	27	91	315
Northern Ireland	Belfast	National Museums Northern Ireland	23			23
Norway	Oslo	Naturhistorisk museum	5	1	4	10
Portugal	Evora	Museu de Evora	3			3
Portugal	Lisbon	Museu Nacional de Historia Natural	30			30
Portugal	Lisbon	Instituto de Investigação Científica Tropical	11			11
Russia	St-Petersburg	Zoological Museum	25	5	4	34
South Africa	Bloemfontein	National Museum	9			9
South Africa	Cape Town	Iziko South African Museum	10			10
South Africa	Durban	Durban Natural Science Museum	45			45
South Africa	East London	East London Museum	47			47
South Africa	Kimberly	McGregor Museum	6			6
South Africa	Pretoria	Transvaal Museum	90	1		91
Spain	Barcelona	Museu Geologic del Seminari de Barcelona	15			15
Spain	Madrid	Museo Nacional de Ciencias Naturales	71	1		72
Spain	Seville	Estacion Biologica de Donana	112	7		119
Sweden	Stockholm	Naturhistoriska riksmuseet	57	27	3	87
Sweden	Uppsala	Evolutions Museet Uppsala Universitet	4			4
Switzerland	Basel	Naturhistorisches Museum Basel	119	3	8	130
Switzerland	Bern	Naturhistorisches Museum Bern	72	16		88
Switzerland	Chaux-de-Fonds	Musée d'Histoire Naturelle	9			9
Switzerland	Fribourg	Musée d'Histoire Naturelle	14			14
Switzerland	Geneva	Musée d'Histoire Naturelle	31	12		43
Switzerland	Lausanne	Musée cantonal de Zoologie	25			25
Switzerland	Neuchâtel	Musée d'Histoire Naturelle	32			32
Switzerland	Zurich	Zoological Museum of the University of Zurich	13		2	15
Tasmania	Hobart	Tasmanian Museum and Art Gallery			4	4
Tasmania	Launceston	Queen Victoria Museum and Art Gallery			8	8
USA (Arizona)	Flagstaff	Museum of Northern Arizona		7		7
USA (Arizona)	Tucson	University of Arizona Museum of Natural History		17		17

USA (California)	Berkeley	Museum of Vertebrate Zoology	1	129	8	138
USA (California)	Camarillo	Western Foundation of Vertebrate Zoology		144	1	145
USA (California)	Los Angeles	UCLA-Dickey Bird and Mammal Collections		24		24
USA (California)	Los Angeles	The Moore Laboratory of Zoology		14		14
USA (California)	Los Angeles	Natural History Museum of Los Angeles County	7	75		82
USA (California)	Redlands	San Bernardino County Museum		15		15
USA (California)	San Diego	San Diego Natural History Museum		56		56
USA (California)	San Francisco	The California Academy of Sciences	1	110	1	112
USA (California)	Santa Barbara	Santa Barbara Museum of Natural History	1	60		61
USA (Colorado)	Denver	Denver Museum of Nature and Science	1	30	1	32
USA (Connecticut)	New Haven	Peabody Museum of Natural History at Yale University	28	37	7	72
USA (Delaware)	Wilmington	Delaware Museum of Natural History	2	22	4	28
USA (District of Columbia)	Washington DC	Smithsonian Institution, Natural Museum of Natural History	48	237	26	311
USA (Florida)	Gainesville	Florida Museum of Natural History, University of Florida	1	51	1	53
USA (Hawaii)	Honolulu	Bishop Museum		28	1	29
USA (Illinois)	Chicago	The Chicago Academy of Sciences and its Peggy Notebaert Nature		15		15
USA (Illinois)	Chicago	The Field Museum of Natural History	58	176	29	263
USA (Kansas)	Lawrence	Natural History Museum and Biodiversity Research Center	1	43	3	47
USA (Louisiana)	Bâton Rouge	Louisiana Museum of Natural Science	1	98		99
USA (Massachussets)	Harward	Harward Museum of Natural History	23	165	14	202
USA (Minnesota)	Minneapolis	The University of Minnesota, Bell Museum of Natural History		11	2	13
USA (Mitchigan)	Ann Arbor	University of Michigan, Museum of Zoology	6	95	1	102
USA (Mitchigan)	East Lansing	Michigan State University Museum		15		15
USA (Montana)	Missoula	Philip L. Wright Zoological Museum		4		4
USA (Nebraska)	Lincoln	University of Nebraska State Museum		15		15
USA (New Mexico)	Albuquerque	Museum of Southwestern Biology		53	1	54
USA (New Mexico)	Las Cruces	The Vertebrate Museum, New Mexico State University		10		10
USA (New York)	Buffalo	Buffalo Museum of Science		10		10
USA (New York)	Cornell	Cornell University	7	29	2	38
USA (New York)	New York	American Museum of Natural History	326	225	232	783
USA (Ohio)	Cleveland	Cleveland Museum of Natural History	2	47		49
USA (Ohio)	Columbus	The Ohio State University		40		40

USA (Oklahoma)	Norman	Sam Noble Oklahoma Museum of Natural History		15		15
USA (Pennsylvania)	Philadelphia	Academy of Natural Sciences	11	65	15	91
USA (Pennsylvania)	Pittsburgh	Carnegie Museum of Natural History	9	62		71
USA (Texas)	Alpine	Sul Ross State University		6		6
USA (Texas)	College Station	Texas A&M University College Station		50	1	51
USA (Texas)	Dallas	Museum of Nature and Science		13		13
USA (Texas)	El Paso	Centennial Museum, University of Texas		11		11
USA (Texas)	Lubbock	Texas Technology University		21		21
USA (Texas)	San Angelo	Angelo State University, Department of Biology		9		9
USA (Utah)	Provo	Young University		16	3	19
USA (Utah)	Salt Lake City	Utah Museum of Natural History		9		9
USA (Washington)	Pullman	Washington State University, Charles R. Conner Museum		61		61
USA (Washington)	Seattle	Burke Museum		69	8	77
USA (Washington)	Tacoma	Slater Museum of Natural History		64		64
USA (Wisconsin)	Madison	University of Wisconsin, Zoological Museum		12		12
Zimbabwe	Bulawayo	Natural History Museum of Zimbabwe	157			157
Private citizen collections			156			156
Total		141	4670	3050	1390	9110

Chapter 6

Geographic variation in body size and plumage colour according to diet composition in a nocturnal raptor

Andrea Romano[1,2], Robin Séchaud[1] and Alexandre Roulin[1†]

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

[2] Department of Environmental Science and Policy, University of Milan, Milano, Italy.

Chapter Status:

Published in Journal of Avian Biology

https://doi.org/10.1111/jav.02716

Author contributions:

All authors conceived the study; A.R.[†] collected the data; A.R. and R.S. performed the statistical analyses; A.R. drafted the manuscript; all the authors contributed to the final version of the paper.

JOURNAL OF
AVIAN BIOLOGY

Article

Geographic variation in body size and plumage colour according to diet composition in a nocturnal raptor

Andrea Romano, Robin Séchaud and Alexandre Roulin

A. Romano (https://orcid.org/0000-0002-0945-6018) ✉ (andrea.romano@unimi.it), R. Séchaud and A. Roulin (https://orcid.org/0000-0003-1940-6927), Dept of Environmental Science and Policy, Univ. of Milan, Milano, Italy. AR also at: Dept of Ecology and Evolution, Univ. of Lausanne, Lausanne, Switzerland.

Journal of Avian Biology
2021: e02716
doi: 10.1111/jav.02716

Subject Editor:
Marcos Robalinho Lima
Editor-in-Chief: Jan-Åke Nilsson
Accepted 15 March 2021

Predator–prey interactions are amongst the strongest selective forces that promote the evolution of local phenotypes in both predators and prey. However, intraspecific spatial covariation in phenotypic traits between predators and prey has been rarely investigated, especially at a large geographic scale. Here, we studied the covariation between prey composition and some phenotypic traits, such as wing length, bill length and plumage colour, of a widely-distributed nocturnal predator, the western barn owl *Tyto alba*. By using 3100 specimens collected across its entire range of distribution, spanning from Europe to Middle East and Africa, we showed that wing length positively covaries with prey size, but not with taxonomic composition. This finding suggests that larger prey might have selected for larger body size and/or that larger individuals might be more selective in hunting large prey. In addition, we also found that paler-plumaged populations generally hunt larger prey. Paler barn owls might be thus better specialized in capturing averagely larger prey and/or mainly hunt in habitats where larger prey are more abundant. In addition, considering that paler individuals are generally larger than brownish ones, it is possible that paler plumage colour might have evolved as a by-product of selection towards a large body size, which in turn have emerged in response to prey size composition. However, irrespectively of the direction of causality and the phenotypic target of selection, we showed that predator–prey interactions can affect spatial phenotypic variation by promoting the evolution of local adaptations.

Keywords: body size, diet diversity, melanin-based colour, predator–prey interactions, predator–prey size

Introduction

Interactions between prey and predators are amongst the major selective forces that drive a diverse suite of functional phenotypes in both counterparts (Kerfoot and Sih 1987, Tollrian and Harvell 1999). Feeding relationships can indeed shape elaborate behavioural, physiological and morphological adaptations to prevail in the evolutionary arms race (Edmunds 1974, Surlykke and Miller 1985, Reimchen 1980, West et al. 1991, Brodie III and Brodie Jr et al. 1999), as well as have a prominent and pervasive impact on the stability of food webs, on the structure of animal communities

NORDIC SOCIETY OIKOS

www.avianbiology.org

---

and on the dynamics of natural populations (Emmerson and Raffaelli 2004, Brose et al. 2006b, Petchey and Dunne 2012).

One of the most recognized patterns of predator–prey interactions, which is consistent across aquatic and terrestrial biomes, is that they are intrinsically size-structured (Emerson et al. 1994, Brose et al. 2006a, Hatton et al. 2015). Indeed, it is generally well acknowledged that a predator's size correlates with its prey size (Vézina 1985, Radloff and Du Toit 2004, Owen-Smith and Mills 2008, Costa 2009). According to the optimal foraging theory (Stephens et al. 2007), large animals should select food items which are generally larger than those usually eaten by small species. However, it is also recognized that predators of limited size are usually forced to hunt small prey items (Brown and Maurer 1989, Barclay and Brigham 1991), partially because their gape is smaller comparing to larger animals (Shine and Sun 2003), while large ones are able to detect, capture and consume prey of more variable sizes (Brown and Maurer 1989, Scharf et al. 2000). In addition, larger species usually live in larger home and geographic ranges than smaller ones, thus potentially encountering a wider variety of prey. According to these premises, a positive association between a predator's body size and its diet niche breadth is expected (Gittleman 1985, Scharf et al. 2000). Such an allometric scaling in the relationships between predator size and prey size and diversity is a crucial aspect of food web and metabolic theories (Emmerson and Raffaelli 2004, Brose et al. 2006b, Otto et al. 2007, Petchey and Dunne 2012, Kalinkat et al. 2013).

It is important also to note that the strength of predator–prey interactions, however, is not constant across time and space. As a consequence, the magnitude of selection on phenotypic traits of predators and prey is expected to fluctuate spatially and temporally, thus promoting the local emergence of functional phenotypes (Van Buskirk 2002, Kishida et al. 2007). Associations between predators and prey phenotypes, especially size, have been widely studied, but most of the current knowledge is based on comparative studies among species (Vézina 1985, Radloff and Du Toit 2004, Owen-Smith and Mills 2008, Costa 2009, but see Török 1993) or within-population analyses (Simpfendorfer et al. 2001, Ingram et al. 2011). However, intraspecific spatial covariation in phenotypic traits between predators and prey has been rarely investigated (Schwaner 1985, Erlinge 1987, Forsman 1991). This is especially the case for species living across wide geographical ranges. This is unfortunate because its examination is fundamental to understanding how local adaptations emerge and potentially drive the evolution of spatial polymorphism (Huey et al. 2000).

To partly fill this gap, in the present study we examined the covariation between prey composition and some phenotypic traits of a widely-distributed nocturnal predator, the western barn owl *Tyto alba*. This species typically hunts small mammals across its entire range of distribution (Romano et al. 2020b), which is comprised between the British Isles and south Scandinavia to South Africa, including Middle East (easternmost point in Iran), Arabian Peninsula, Madagascar, most of the Mediterranean islands and most of the African archipelagos in the Atlantic and Indian Oceans (Romano et al. 2019, 2020a for details). In particular, we investigated whether wing length, a good proxy of body size, bill length and plumage colouration vary geographically according to some diet features, such as percentage of mammals, prey size and diversity. In this taxon, body size (i.e. wing length) does not vary along geographic or climatic gradients according to Bergmann's rule (Romano et al. 2021a), thus suggesting that other selective pressures may drive its spatial variation. Conversely, bill length has been shown to vary consistently with Allen's rule, with populations living at higher latitudes and altitudes (and smaller temperatures) showing a smaller beak than those inhabiting closer to the equator (Romano et al. 2020a). However, considering the obvious importance of this trait in consuming prey, it might be also locally affected by diet. Finally, the degree of brownish colouration has been shown to be not only associated to climatic conditions (Romano et al. 2019), but also to foraging behaviour within population (Roulin 2004, Charter et al. 2012, San-Jose et al. 2019), therefore leaving open the possibility that it is potentially affected by local diet.

According to the previous literature, we predicted that wing length and bill length should be positively associated with prey size. Indeed, larger individuals with a larger bill should be better able to hunt and process larger prey. Because small predators are often restricted in hunting small prey, we also expected that wing length and bill length should be positively associated with prey diversity. Finally, given the lack of scientific literature on these topics, we refrain from proposing specific predictions for the other relationships between phenotypic traits and diet features.

Methods

Diet data collection

Diet data were collected using published information extracted from scientific papers, grey literature and PhD/master theses reporting description of pellets content (details in Romano et al. 2020b). We then selected the papers/reports collecting at least 90 vertebrate prey (Marti et al. 2007), and in which at least of 80% of mammalian prey were identified at the genus level. Following Romano et al. (2020b), we also included diet data of a small island in Cape Verde archipelago (Fogo island, Siverio et al. 2008) with a smaller sample size (50 identified prey). However, the results are qualitatively very similar excluding this datum. We retained papers including information collected in a single site and in geographical small regions (e.g. island, county, district), as well as studies including single-year and multiple-year data. Following Romano et al. (2020b), in order to reduce the temporal variability in diet composition, analyses were limited to data collected after 1940.

For every location, we reported the geographical coordinates, and the proportion of each terrestrial mammalian prey genus *i* (number of individuals of genus *i* divided by the total number of terrestrial mammals contained in the pellets) was recorded. When reported, the proportion of the terrestrial mammalian prey over the total amount of vertebrate prey was also computed. Because many studies focused on non-volant mammals only and considering that they represent a minor component of the barn owl's diet (Roulin and Christe 2013), bats were included among the other vertebrates, with birds, reptiles and amphibians. Information on invertebrates was discarded because a very small part of the papers reported reliable information about this food source and because it contributes to a minimal part to the diet (Obuch and Benda 2009, Muñoz-Pedreros et al. 2016, Romano et al. 2020b for details).

Because many studies did not include information at the species level and in order to account for variability in the species diversity among genera, Shannon diversity index of prey was calculated at the genus level (i.e. using the proportion of each mammalian prey genus). The Shannon diversity index was calculated only on mammals because they are the major component of barn owl diet and because in many cases the other vertebrates were generically reported as birds, reptiles or amphibians (Romano et al. 2020b for details). We used Shannon diversity index because it is a good proxy for summarizing diet diversity, irrespectively of prey taxonomy, as reported by recent studies in raptors, including the species under investigation (Milana et al. 2018, Janžekovič and Klenovšek 2020, Romano et al. 2020b). Finally, average body mass of each mammalian prey genus was also estimated. Then, prey were coded into four categories depending on their size (small = maximum 25 g, medium = between 26 and 50 g, large = between 51 and 100 g, very large = more than 100 g). Further detailed information are reported in Romano et al. (2020b).

Collection of phenotypic data

Information on wing length, bill length and degree of reddish colouration of the breast was collected on thousands of *T. alba* specimen across Europe, Middle East and Africa, which were deposited in museums or collected by private citizens (Romano et al. 2019, 2020a for details). All measurements were made by the same experimenter (A. Roulin). Wing and bill length were measured to the nearest 1 mm and 0.1 mm, respectively, and their measurements are highly repeatable (Romano et al. 2020a). Importantly, we used wing length as a predictor of body size because information on other traits associated with body size (e.g. body mass) was not available on museum specimens and because the vast majority of the studies investigating body size variation in birds used this trait as a surrogate for size (Ashton 2002). Also, this trait was used for the same purpose in previous analyses of the species under investigation (Romano et al. 2021a, Romano et al. in press). The plumage colour of the underside region of the body, which varies from white to reddish-brown both among and within populations (Supporting information; Roulin 2003, Romano et al. 2019), was categorized on an 8-level scale, ranging from 1 for dark brownish to 8 for white. Hereafter, we refer to dark/darker and pale/paler individuals according to this white-to-brown categorization of plumage colour. This categorization is a reliable information on the feather colour because it strictly mirrors the reflectance in the range of visible light as measured by a spectrometer (Dreiss and Roulin 2010). For all the specimens, we also collected geographical coordinates of the location where they were collected.

Association between diet and phenotypic data

We then combined the above-described datasets with the following procedure. Firstly, we divided the distribution range of *T. alba* into cells of variable side length, from 100 to 400 km. Within each cell we pooled all the diet information provided by different studies. For example, when in a 200 by 200 km cell there were three sites where diet information was available, they were pooled in order to combine all the information about diet data in the same region. We simply averaged the values of different prey categories per site within each cell (e.g. mean proportion of small prey, mean Shannon diversity index, mean proportion of mammals). However, considering that different studies collected information on different sample size (range: 50–233 540 prey items per site, median: 904 prey items per site), with a second procedure, we summed up all the data from different sites (i.e. sum of small mammals, sum of vertebrates, sum of mammal prey, etc…) and then computed a global value for every diet parameter within each cell. This procedure allowed us to weigh more diet data collected in sites where a larger sampling effort was done. Analyses were performed using data extracted with both procedures, but in the Results section we only show the results obtained using the mean values of each diet parameters, while the others are reported in the Supporting information.

To each cell we also associated the barn owl specimens whose coordinates of the recovery site were contained within the cell. However, when diet information was available for islands smaller than a 200 by 200 km cell, we associated to each datum only phenotypic data of the barn owl inhabiting that given island. Again, we averaged values of phenotypic traits among specimens within each cell. Considering that the barn owl shows moderate phenotypic variability within populations, we only considered cells that had data on at least four specimens to increase the accuracy on phenotypic information.

We repeated this procedure for cells of different size (100, 200 and 400 km side length). After this step, the sample size of locations was adequate to perform analyses for cells of 100 and 200 km side length. For the analyses, we considered cells of 200 km side length as the best compromise between a large geographical coverage of the diet data, a large sample size and an accurate estimate of barn owl's phenotype. This is why analyses using such a spatial scale were reported in the main text. However, analyses were repeated on cells of 100 km to check whether results were consistent using different scales. Unfortunately, we could not do the same for cells of 400 km side length because of a considerable reduction of the sample size (a reduction of ca 30% of cells) and because the geographic coverage of data was extremely biased towards Europe.

On the whole, our analyses included 116 cells containing on average 17.27 barn owls (range: 4–229, Supporting information). However, sample sizes of different phenotypic traits slightly vary because of missing data (e.g. bill was broken, wingless individuals, etc…). The total number of barn owl specimens in the analyses is 3100 and the total mammal prey items identified in the locations included in the analyses is 723 556.

Statistical analyses

To examine variation in phenotypic traits according to diet parameters, we used linear models using the 'glmmTMB' package (Brooks et al. 2017) in R (ver. 3.5.1). Variation in wing length, bill length and plumage colour was analysed separately (Romano et al. 2019, 2020a), including Shannon diversity index, and proportion of small prey (up to 25 g) as predictors. We focused on proportion of small prey rather than on average size of the prey for two important reasons. First, prey size was estimated at the genus level and this information is therefore not precise enough to properly obtain an accurate estimate of average prey size. This is not the case for proportion of small prey because each genus considered in the analyses is included in a single size category. Second, average prey size can be considerably affected by the presence of a small number of prey items of extreme size, while this is not the case for proportion of small prey.

We note that we chose a different cut-off of prey size (25 g rather than 50 g) compared to the one used in a previous study that focused on different barn owl lineages living in other continents (Romano et al. 2020b) for a specific reason: prey size is generally much smaller in the regions inhabited by *T. alba* than those inhabited by the other barn owl lineages (i.e. *T. furcata* and *T. javanica*), and prey smaller than 50 g comprised more than 90% of the prey almost everywhere in its distribution range (Romano et al. 2020b). In practice, *T. alba* almost entirely relies on prey smaller than 50 g, and using such a cut-off the distribution of this predictor is highly biased toward higher values. This is not the case for a 25 g cut-off, which results in a normal distribution of this predictor. In the present study, we could not include analyses on the other barn owl lineages because of small sample size.

In addition, we repeated the analyses also including proportion of mammals in the diet. However, because proportion of mammals was never a significant predictor (Results) and considering that this information was not available for all the cells (i.e. some diet studies were focused on mammals only), thus resulting in a reduction of sample size, the final analyses were repeated excluding this term. Although within single population, darker owls seem to consume more cricetids and paler more murids (Roulin 2004, Charter et al. 2012), an analysis at such a low taxonomic level (i.e. the family level) were prevented because of the large diversity of small mammal assemblages across the distribution range of the barn owl. For example, no cricetids have been reported in the diet of African barn owls (Romano et al. 2020b), thus preventing us to perform proper analyses on this.

Since both phenotype and diet vary between islands and mainland (Romano et al. 2019, 2020a, b, Romano et al. in press, Janžekovič and Klenovšek 2020), in the models we also included a dichotomic factor indicating if the cell under investigation was on an island (coded as 1) or a mainland (coded as 0). However, analyses performed on continental populations only provided very similar results to those shown in the Result section (details not shown).

Diet and phenotypic traits are not randomly distributed across space (Romano et al. 2019, 2020a, b). In order to account for non-random distribution of locations, in all the models we also accounted for spatial autocorrelation, by adding an exponential correlation structure considering the distances between all the pairs of latitude–longitude coordinates of the centre of each cell.

The phenotypic traits under investigation have been shown to be predicted by climatic factors, such as temperature and precipitation (Romano et al. 2019, 2020a), potentially affecting our results. The models described above were therefore repeated with the inclusion of mean annual temperature and annual rainfall of the centroid of each cell, extracted from the WordClim data repository (<http://www.worldclim.org/>, Fick and Hijmans 2017) for the period 1970–2000 (for details, Romano et al. 2019, 2020a), as additional predictors. In order to check whether significant diet predictors were included in all the best supported models (in terms of Akaike information criterion; AIC hereafter), we also performed a model selection analysis for each dependent variable, using function *dredge* of the R package 'MuMIn' (Barton 2009).

For all the models, we checked for collinearity (i.e. variance inflation factor), residual diagnostics, normal distribution and homoscedasticity, by using the 'performance' package (Lüdecke et al. 2020). No collinearity (variance inflation factor was always smaller and 2.24) and heteroscedasticity was detected, and the distribution of the model residuals was normal. We finally checked for the presence of outliers (Grubb's test) which were removed from the final models (this was the case for two datapoints in the analyses of wing length).

Results

Wing length is negatively predicted by the proportion of prey smaller than 26 g (Table 1, Fig. 1a). This result implies that body size is larger when the diet is composed mainly of large prey. In addition, a similar pattern was observed when in the same model the proportion of small prey was replaced by mean prey size (slope ± SE = 0.146 ± 0.045; t = 3.24; p = 0.012). No effect of diet diversity (Table 1) and proportion of mammals (slope ± SE = −2.924 ± 3.176; t = −0.92; p = 0.36) was observed on wing length.

Bill length was not affected by any of the predictors (Table 1). This was also the case when wing length was added to the models as an additional predictor in order to test variation in relative bill size (details not shown).

Variation in plumage colour is also significantly affected by the proportion of small prey (Table 1). Indeed, plumage

Table 1. Variation in wing length, bill length and ventral plumage colour according to diet parameters and island versus continental barn owls in cells of 200 km side length.

	Coefficient (SE)	t	p
Wing length			
R^2	0.177		
Intercept	293.524 (3.439)		
Island	1.097 (1.242)	0.88	0.37
Shannon diversity index	−1.136 (0.867)	−1.31	0.19
Proportion of small prey	−5.122 (2.098)	−2.44	0.015
Bill length			
R^2	0.084		
Intercept	192.117 (2.425)		
Island	0.167 (1.276)	0.13	0.90
Shannon diversity index	0.491 (0.774)	0.63	0.53
Proportion of small prey	−1.178 (1.996)	−0.89	0.37
Plumage colour			
R^2	0.616		
Intercept	4.674 (0.760)		
Island	1.111 (0.255)	4.36	< 0.001
Shannon diversity index	0.149 (0.155)	0.96	0.34
Proportion of small prey	−1.194 (0.388)	3.07	0.002

colour becomes darker at increasing proportion of small prey (Fig. 1b). However, mean prey size did not predict variation in this plumage trait (slope ± SE = 0.013 ± 0.009; t = 1.50; p = 0.13). No effect of diet diversity (Table 1) and proportion of mammals (slope ± SE = −0.059 ± 0.549; t = −0.11; p = 0.91) was shown on plumage colour.

Very similar results were obtained when diet parameters were collected in cells of 100 km side, but the signs of the models of bill length were opposite (Supporting information), and when they were summed up from different sites within cell rather than averaged (Supporting information). In the latter analysis, however, wing length also increases with Shannon index. The same statistically significant relationships were obtained when climatic variables were included in the models as additional predictors (Supporting information), thus indicating that the above results are not determined by a covariation between diet, phenotype and climate. This result was confirmed by model selection analyses because all the best supported models in terms of AIC always included proportion of small prey among predictors (Supporting information). The other predictors that were always present in the best supported models of wing length and plumage colour were annual precipitation and island, respectively (Supporting information).

Finally, significant trends in both wing length and plumage colour according to percentage of small prey were found also when the analyses were restricted to prey which are rodents (wing length: slope ± SE = −5.149 ± 2.042; t = −2.52; p = 0.012; plumage colour: slope ± SE = −1.189 ± 0.387; t = −3.07; p = 0.002). Therefore, these patterns are not due to the presence of insectivores in the diet (e.g. Soricidae and Afrosoricidae), which represent a non-negligible fraction of the diet at temperate and boreal regions (Romano et al. 2020b), and which are generally smaller than rodents (Cotgreave and Stockley, 1994).

Discussion

One of the main results found in the present study on a very large geographic scale was that populations of the western barn owl that had longer wings hunted larger prey compared to those showing on averagely smaller wings. This finding is in line with most of interspecific comparative studies (Vézina 1985, Radloff and Du Toit 2004, Owen-Smith and Mills 2008, Costa 2009, but see Török 1993) and within-population analyses (Simpfendorfer et al. 2001, Ingram et al. 2011) showing a predator–prey size allometric scaling, and suggests that large individuals are able to exploit a larger fraction of the encountered prey, including large ones. This pattern can be therefore interpreted as an adaptation of barn owl body size for an efficient use of the available sources of food. Indeed, the net energy gain per prey item consumed is expected to increase with increasing prey size, although larger prey are probably more costly to consume and/or to hunt.

Given the correlative nature of the data, however, we are not in the position of arguing causality in the observed covariation between prey and predator size. Indeed, on the one hand, populations composed of generally large individuals might be specialized in foraging on relatively large prey, and, vice versa, those consisting mainly of small individuals might be constrained to preferentially hunt smaller mammals, possibly because their gape size is small (Shine and Sun 2003). On the other hand, the presence of different prey assemblages might have driven the evolution of large-bodied barn owls in regions where prey are generally larger by exerting a negative selection on smaller individuals and/or because larger prey confer more nutrients thus potentially promoting a larger body size growth. In addition, we cannot exclude the possibility that the observed association would be on wing length per se, and not via an effect on body size. Indeed, wing shape and length are known to considerably affect flight ability and foraging strategies (Gamauf et al. 1998, Corvidae et al. 2006). For example, it is possible that long-winged birds are more specialized in hunting large prey, which should generally cover longer distances in a unit of time. Body size, wing morphology and hunting strategy may thus have coevolved in different populations in order to maximize success in hunting the most available prey. However, irrespectively of the direction of causality and the phenotypic target of selection, our study is the first, to the best of our knowledge, to show an intraspecific spatial variation in body size of a predatory bird according to variation in diet size composition. It adds to the limited known cases of adaptations of predator body size according to the size distribution of prey, which was previously observed in other vertebrate taxa, such as mammals (Erlinge 1987) and snakes (Schwaner 1985, Forsman 1991).

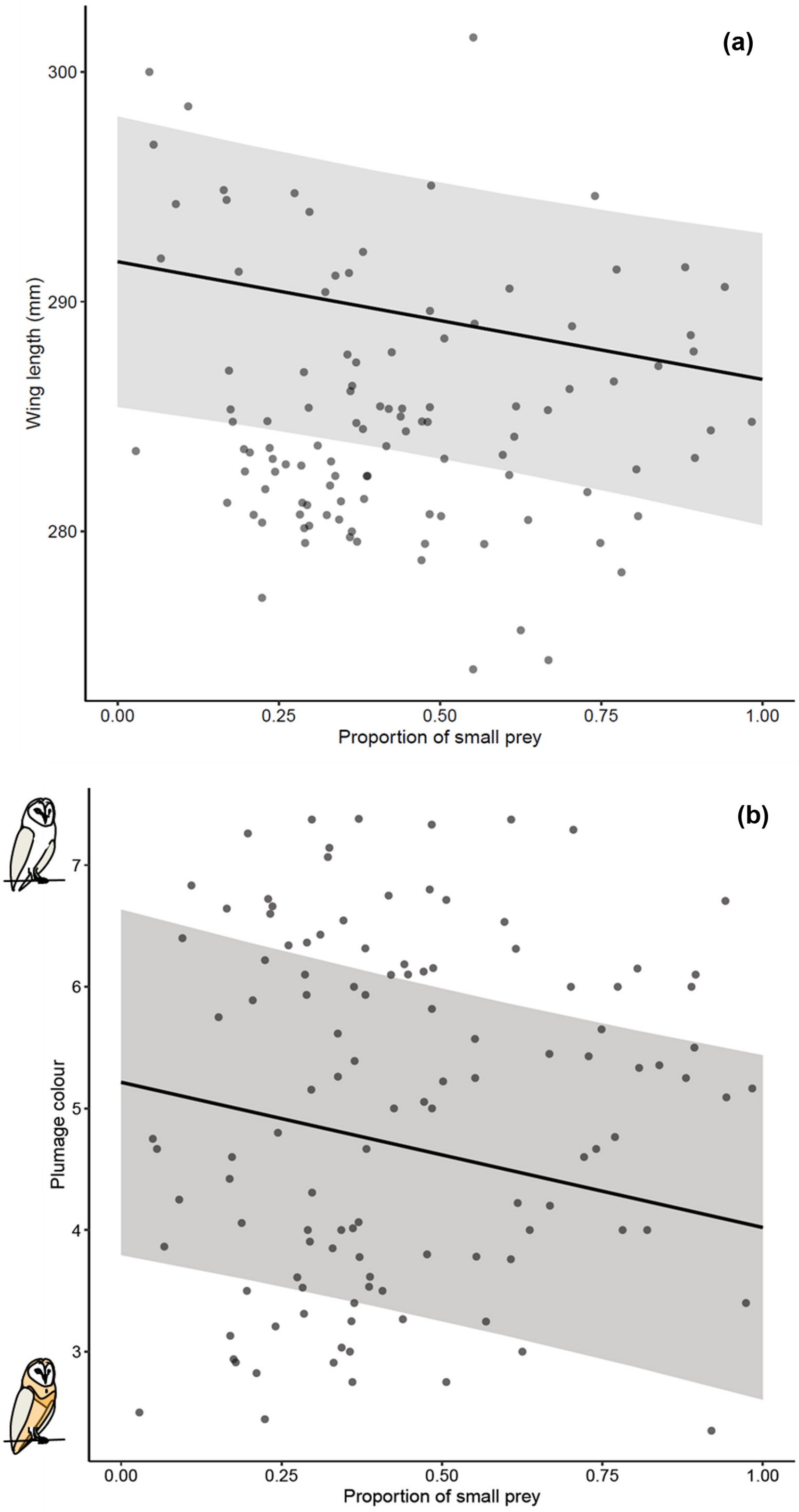


Figure 1. Variation in wing length (panel a) and plumage colour (panel b; smaller values indicate darker plumage) according to the proportion of prey smaller than 25 g in the diet. Regression lines and confidence intervals are the estimates of the models reported in Table 1, and other predictors were fixed as their mean values.

This result also helps to understand and interpret better our recent finding about the lack of any clear variation in wing length along geographic and climatic gradients in *T. alba*, a contrasting result when compared to other species of the same genus (Romano et al. 2021a). Wing length seems therefore more strongly affected by diet composition, and thus on food availability, than climatic factors, at least in this taxon.

Contrary to our expectations, we cannot find any significant trend in (relative and absolute) bill length according to diet parameters, even if the direction of the relationship between bill length and prey size is negative. Although such a result seems surprising, this is not if we consider the hunting behaviour of the barn owl. Indeed, this predator attacks prey using its claws, rather than the bill, and then consumes them after reducing the prey into small pieces (Csermely et al. 2002). While bill shape certainly evolved in response to the typical carnivore diet of the barn owl, intraspecific variation in bill size has therefore been mainly driven by thermoregulation reasons (Romano et al. 2020a), rather than on local prey composition.

Another interesting result disclosed by our analyses is that larger prey are present at a larger proportion in the diet of populations showing paler plumage. How to explain this result is matter of speculation. Considering that foraging behaviour but also hunting habitats have been shown to vary according to plumage colour morphs within population (Charter et al. 2012, San-Jose et al. 2019), it is possible that paler-plumaged barn owls might be better specialized in capturing averagely larger prey and/or mainly hunt in habitats where larger prey are more abundant. An alternative scenario rests on the possibility that paler plumage colour might have evolved as a by-product of selection towards a large body size, which in turn have emerged in response to prey size composition. Indeed, it has been shown that within-population paler individuals are generally heavier than more reddish ones (Roulin 2006). The same relationship between plumage colour and body size (i.e. wing length) also emerges among-population in the sample of barn owls studied here (slope ± SE = 0.048 ± 0.019; $t = 2.59$; $p = 0.010$), thus making such a possibility valid. Finally, we note that a possible causal link between diet and plumage melanisation exists. Indeed, quality and quantity of food ingested seem to have direct effects on melanin plumage traits (McGraw et al. 2002, Poston et al. 2005, McGraw 2007, Galván et al. 2019), with individuals consuming a larger content of dietary amino acids and minerals showing more melanic feathers. Following the above reasoning and considering that larger prey contain more nutrients, brownish, rather than paler, feathers should be typical of individuals eating large prey. Our result is therefore in contrast with this previously suggested link between diet and plumage colour. However, we note that in the barn owl plumage colouration is mainly determined by genetic, than environmental, factors (Roulin and Dijkstra 2003), thus making such a link less likely at least in this species.

Finally, contrarily to our expectations, we did not find any effect of diet diversity or taxonomic composition on any of the phenotypic traits under investigation. A possibility is that our Shannon diversity index computed on mammal genera only did not properly mirror the entire range of the prey consumed by different populations. Taken together, these results thus indicate the main driver of local phenotypic variation is the size of the prey, rather than its taxonomic composition.

In conclusion, we found a covariation between prey size and predator size and melanisation across the distribution range of in a widely-distributed bird predator. Irrespectively of the direction of causality and the phenotypic target of selection, the present study shows that predator–prey interactions are important drivers of spatial phenotypic variation by promoting the evolution of local adaptations. Future studies combining information on prey size and composition at different spatial and temporal scales are needed to test for the generality of the patterns documented here for the barn owl.

Transparent Peer Review

The peer review history for this article is available at https://publons.com/publon/10.1111/jav.02716

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.v15dv41vw> (Romano et al. 2021b).

Author contributions

Andrea Romano: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (equal); Writing – original draft (lead). **Robin Séchaud**: Formal analysis (supporting); Visualization (equal); Writing – original draft (supporting). **Alexandre Roulin**: Data curation (equal); Funding acquisition (lead); Resources (lead); Writing – original draft (supporting).

References

Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. – Global Ecol. Biogeogr. 11: 505–523.

Barclay, R. M. and Brigham, R. M. 1991. Prey detection, dietary niche breadth and body size in bats: why are aerial insectivorous bats so small? – Am. Nat. 137: 693–703.

Barton, K. 2009. MuMIn: multi-model inference. – <http://r-forge.r-project.org/projects/mumin/>.

Brodie III, E. D. and Brodie Jr, E. D. 1999. Predator–prey arms races: asymmetrical selection on predators and prey may be reduced when prey are dangerous. – Bioscience 49: 557–568.

Brooks, M. E. et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – R J. 9: 378–400.

Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L. F., ... and Cohen, J. E. 2006a. Consumer–resource body-size relationships in natural food webs. – Ecology 87: 2411–2417.

Brose, U., Williams, R. J., and Martinez, N. D. 2006b. Allometric scaling enhances stability in complex food webs. – Ecol. Lett. 9: 1228–1236.

Brown, J. H. and Maurer, B. A. 1989. Macroecology: the division of food and space among species on continents. – Science 243: 1145–1150.

Charter, M. et al. 2012. Similar patterns of local barn owl adaptation in the Middle East and Europe with respect to melanic coloration. – Biol. J. Linn. Soc. 106: 447–454.

Corvidae, E. L. et al. 2006. Comparison of wing morphology in three birds of prey: correlations with differences in flight behavior. – J. Morphol. 267: 612–622.

Costa, G. C. 2009. Predator size, prey size and dietary niche breadth relationships in marine predators. – Ecology 90: 2014–2019.

Cotgreave, P. and Stockley, P. 1994. Body size, insectivory and abundance in assemblages of small mammals. – Oikos 71: 89–96.

Csermely, D. et al. 2002. Adaptive details in the comparison of predatory behaviour of four owl species. – Ital. J. Zool. 69: 239–243.

Dreiss, A. and 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. – Biol. J. Linn. Soc. 101: 689–704.

Edmunds, M. 1974. Defence in animals: a survey of anti-predator defences. – Longman Publishing Group.

Emerson, S. B. et al. 1994. Allometric aspects of predator–prey interactions. – Ecol. Morph. 73: 123–139.

Emmerson, M. C. and Raffaelli, D. 2004. Predator–prey body size, interaction strength and the stability of a real food web. – J. Anim. Ecol. 73: 399–409.

Erlinge, S. 1987. Why do European stoats *Mustela erminea* not follow Bergmann's rule? – Ecography 10: 33–39.

Fick, S. E. and Hijmans, R. J. 2017. Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. – Int. J. Clim. 37: 4302–4315.

Forsman, A. 1991. Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. – J. Anim. Ecol. 60: 253–267.

Galván, I. et al. 2019. Pheomelanin synthesis varies with protein food abundance in developing goshawks. – J. Comp. Phys. B 189: 441–450.

Gamauf, A. et al. 1998. Philippine birds of prey: interrelations among habitat, morphology and behavior. – Auk 115: 713–726.

Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. – Oecologia 67: 540–554.

Hatton, I. A. et al. 2015. The predator–prey power law: biomass scaling across terrestrial and aquatic biomes. – Science 349: 6252.

Huey, R. B., Gilchrist, G. W., Carlson, M. L., Berrigan, D., and Serra, L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. – Science 287: 308–309.

Ingram, T. et al. 2011. Does intraspecific size variation in a predator affect its diet diversity and top–down control of prey? – PLoS One 6: e20782.

Janžekovič, F. and Klenovšek, T. 2020. The biogeography of diet diversity of barn owls on Mediterranean islands. – J. Biogeogr. 47: 2353–2361.

Kalinkat, G. et al. 2013. Body masses, functional responses and predator–prey stability. – Ecol. Lett. 16: 1126–1134.

Kerfoot, W. C. and Sih, A. 1987. Predation: direct and indirect impacts on aquatic communities. – Univ. Press of New England, Hanover.

Kishida, O., et al. 2007 Geographic variation in a predator-induced defense and its genetic basis. – Ecology 88: 1948–1954.

Lüdecke, D., Makowski, D., Waggoner, P. and Patil, I. 2020. performance: assessment of regression models performance. – CRAN. doi: 10.5281/zenodo.3952174, R package, <https://easystats.github.io/performance/>.

Marti, C. D., Bechard, M. and Jaksic, F. M. 2007. Food habits. – In: Raptor research and management techniques. Raptor Research Foundation Hancock House Canada, pp. 129–151.

McGraw, K. J. 2007. Dietary mineral content influences the expression of melanin-based ornamental coloration. – Behav. Ecol. 18: 137–142.

McGraw, K. J. et al. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. – J. Exp. Biol. 205: 3747–3755.

Milana, G. et al. 2018. Forty years of dietary studies on barn owl *Tyto alba* reveal long term trends in diversity metrics of small mammal prey. – Anim. Biol. 68: 129–146.

Muñoz-Pedreros, A. et al. 2016. Trophic ecology of two raptors, barn owl *Tyto alba* and whitetailed kite *Elanus leucurus*, and possible implications for biological control of hantavirus reservoir in Chile. – Wilson J. Ornit. 128: 391–403.

Obuch, J. and Benda, P. 2009. Food of the barn owl *Tyto alba* in the eastern Mediterranean. – Slovak Raptor J. 3: 41–50.

Otto, S. B. et al. 2007. Allometric degree distributions facilitate food-web stability. – Nature 450: 1226–1229.

Owen-Smith, N. and Mills, M. G. 2008. Predator–prey size relationships in an African large-mammal food web. – J. Anim. Ecol. 77: 173–183.

Petchey, O. L. and Dunne, J. A. 2012. Predator–prey relations and food webs. – Metab. Ecol. A Scaling Appr.: 86–98.

Poston, J. P., et al. 2005. Dietary amino acids influence plumage traits and immune responses of male house sparrows, *Passer domesticus*, but not as expected. – Anim. Behav. 70: 1171–1181.

Radloff, F. G. and Du Toit, J. T. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. – J. Anim. Ecol. 73: 410–423.

Reimchen, T. E. 1980. Spine deficiency and polymorphism in a population of *Gasterosteus aculeatus*: an adaptation to predators? – Can. J. Zool. 58: 1232–1244.

Romano, A. et al. 2019. Climate-driven convergent evolution of plumage colour in a cosmopolitan bird. – Global Ecol. Biogeogr. 28: 496–507.

Romano, A. et al. 2020a. Geographical variation in bill size provides evidence for Allen's rule in a cosmopolitan raptor. – Global Ecol. Biogeogr. 29: 65–75.

Romano, A. et al. 2020b. Global biogeographical patterns in the diet of a cosmopolitan avian predator. – J. Biogeogr. 47: 1467–1481.

Romano, A. et al. 2021a. Generalized evidence for Bergmann's rule body size variation in a cosmopolitan owl genus. – J. Biogeogr. 48: 51–63.

Romano, A., Séchaud, R. and Roulin, A. 2021b. Data from: Geographic variation in body size and plumage colour according to diet composition in a nocturnal raptor. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.v15dv41vw>.

Romano, A., Séchaud, R. and Roulin, A. 2021b. Evolution of wing length and melanin-based coloration in insular populations of a cosmopolitan raptor. – Journal of Biogeography, <https://doi.org/10.1111/jbi.14053>.

Roulin, A. 2003. Geographic variation in sexually selected traits: a role for direct selection or genetic correlation? – J. Avian Biol. 34: 251–258.

Roulin, A. 2004. Covariation between plumage colour polymorphism and diet in the barn owl *Tyto alba*. – Ibis 146: 509–517.

Roulin, A. 2006. Linkage disequilibrium between a melanin-based colour polymorphism and tail length in the barn owl. – Biol. J. Linn. Soc. 88: 475–488.

Roulin, A. and Christe, P. 2013. Geographic and temporal variation in the consumption of bats by European barn owls. – Bird Study 60: 561–569.

Roulin, A. and Dijkstra, C. 2003. Genetic and environmental components of variation in eumelanin and phaeomelanin sex-traits in the barn owl. – Heredity 90: 359–364.

San-Jose, L. M. et al. 2019. Differential fitness effects of moonlight on plumage colour morphs in barn owls. – Nat. Ecol. Evol. 3: 1331–1340.

Scharf, F. S. et al. 2000. Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. – Mar. Ecol. Prog. Ser. 208: 229–248.

Schwaner, T. D. 1985. Population structure of black tiger snakes, Notechis ater niger, on offshore islands of South Australia. Pp 35–46. In G. Grigg, R. Shine, and H. Ehmann (Eds.), Biology of Australian Frogs and Reptiles. Royal Zoological Society of New South Wales, Sydney, Australia

Shine, R. and Sun, L. X. 2003. Attack strategy of an ambush predator: which attributes of the prey trigger a pit-viper's strike? – Funct. Ecol. 17: 340–348.

Simpfendorfer, C. A. et al. 2001. Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from western Australian waters. – Environ. Biol. Fishes 61: 37–46.

Siverio, F. et al. 2008. Notes on the diet of *Tyto alba* in two oceanic islands from the Mid-Atlantic, Porto Santo and Fogo (Aves: Tytonidae). – Vieraea 36: 163–165.

Stephens, D. W. et al. 2007. Foraging: behavior and ecology. – Univ. of Chicago Press.

Surlykke, A. and Miller, L. A. 1985. The influence of arctiid moth clicks on bat echolocation: jamming or warning? – J. Comp. Phys. A 156: 831–843.

Tollrian, R. and Harvell, C. D. 1999. The ecology and evolution of inducible defenses. – Princeton Univ. Press.

Török, J. 1993. The predator–prey size hypothesis in three assemblages of forest birds. – Oecologia 95: 474–478.

Van Buskirk, J. 2002. A comparative test of the adaptive plasticity hypothesis: relationships between habitat and phenotype in anuran larvae. – Am. Nat. 160: 87–102.

Vézina, A. F. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. – Oecologia 67: 555–565.

West, K. et al. 1991. Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator–prey coevolution. – Evolution 45: 589–607.

Chapter 6 – Supplementary information

Figure S1. An example of the variation in plumage colouration in the Western barn owl *Tyto alba*. Barn owls display continuous variation in plumage colouration from immaculate white to dark reddish pheomelanic. Author: Alexandre Roulin

Figure S2. Geographic distribution of 200 by 200 km cells for which both barn owl diet and phenotypic information was available.

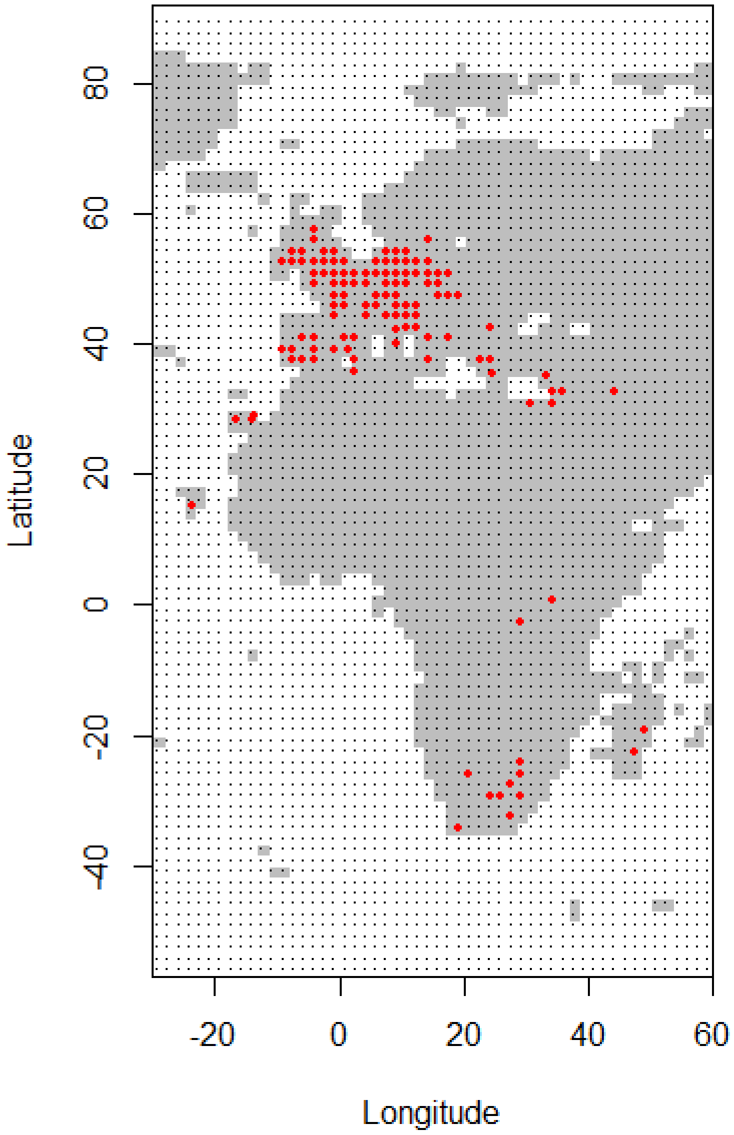


Table S1. Variation in wing length, bill length, and ventral plumage colour according to diet parameters and island vs. continental barn owls in cells of 100 km side length.

	Coefficient (SE)	t	P
Wing length			
Intercept	291.983 (2.873)		
Island	1.380 (1.588)	0.87	0.38
Shannon diversity Index	-0.592 (0.953)	-0.62	0.53
Proportion of small prey	-5.257 (2.0304)	-2.28	0.023
Bill length			
Intercept	191.151 (2.816)		
Island	-0.350 (1.421)	-0.25	0.81
Shannon diversity Index	-0.085 (0.780)	-0.11	0.91
Proportion of small prey	0.133 (1.978)	0.01	0.99
Plumage colour			
Intercept	4.534 (0.586)		
Island	1.062 (0.299)	3.55	<0.001
Shannon diversity Index	0.229 (0.166)	1.38	0.17
Proportion of small prey	-1.170 (0.415)	-2.82	0.005

Table S2. Variation in wing length, bill length, and ventral plumage colour according to diet parameters and island vs. continental barn owls when diet parameters were summed up from different sites within cells of 200 km side length rather than averaged.

	Coefficient (SE)	t	P
Wing length			
Intercept	291.523 (3.083)		
Island	1.858 (1.234)	1.51	0.13
Shannon diversity Index	0.099 (0.048)	2.04	0.041
Proportion of small prey	-5.845 (2.020)	-2.89	0.004
Bill length			
Intercept	192.710 (2.169)		
Island	0.0414 (1.248)	0.03	0.97
Shannon diversity Index	0.031 (0.045)	0.69	0.49
Proportion of small prey	-1.583 (1.973)	-0.80	0.42
Plumage colour			
Intercept	4.867 (0.721)		
Island	1.074 (0.251)	4.28	<0.001
Shannon diversity Index	0.008 (0.009)	0.84	0.40
Proportion of small prey	-1.125 (0.379)	-2.97	0.003

Table S3. Variation in wing length, bill length, and ventral plumage colour according to diet parameters and island vs. continental barn owls, as well as mean annual temperature and annual precipitation.

	Coefficient (SE)	t	P
Wing length			
Intercept	281.215 (8.866)		
Island	0.730 (1.284)	0.57	0.57
Shannon diversity Index	-0.807 (1.048)	-0.77	0.44
Proportion of small prey	-6.352 (2.721)	-2.33	0.020
Mean annual temperature	0.562 (0.460)	1.22	0.22
Annual precipitation	0.003 (0.001)	2.19	0.028
Bill length			
Intercept	185.204 (5.10)		
Island	0.086 (1.258)	0.07	0.95
Shannon diversity Index	0.591 (0.803)	0.74	0.46
Proportion of small prey	-2.173 (1.982)	-1.10	0.27
Mean annual temperature	0.290 (0.245)	1.24	0.22
Annual precipitation	0.002 (0.002)	1.41	0.16
Plumage colour			
Intercept	4.914 (1.166)		
Island	1.129 (0.250)	4.51	<0.001
Shannon diversity Index	0.192 (0.155)	1.24	0.21
Proportion of small prey	-1.190 (0.381)	-3.13	0.002
Mean annual temperature	0.017 (0.047)	0.37	0.71
Annual precipitation	-0.0008 (0.0004)	-2.02	0.044

Table S4. Akaike information criterion and predictors included in the most supported models (all the models showing AIC ≤ 2 referred to the best model) after dredge procedure for wing size, bill size and plumage colour. PSP = proportion of small prey; SDI = Shannon diversity index; T = mean annual temperature; P = annual precipitation; I = island.

	Predictors	AIC
Wing length	PSP + T + P	606.3
	PSP + SDI + T + P	607.3
	PSP + T + P + I	607.3
	PSP + SDI + P	607.7
Bill length		
	P	584.1
	PSP	585.3
	SDI	585.7
	I	585.9
Plumage colour		
	PSP + P + I	274.1
	PSP + SDI + P + I	274.7
	PSP + I	276.0
	PSP + T+ P + I	276.1

General Discussion

The variation of noticeable phenotypic traits within species has long fascinated evolutionary biologists and naturalists, as have the mechanisms underlying their evolution and maintenance (Levins, 1979; Mayr, 1963; Sobel et al., 2010). Colouration has probably attracted the most attention as it is conspicuous and easily measurable. Colour polymorphic species in particular are ideal to study the selective pressures maintaining diversity, as well as the adaptive function of the polymorphic trait (Galeotti et al., 2003; Roulin, 2004b). Local adaptation plays a crucial role in maintaining intra-specific genetic and phenotypic variation (Gavrilets, 2003; Levene, 1953), with resident individuals displaying specific adaptations to local environmental conditions (Williams, 1966).

In the present thesis, I investigated the mechanisms maintaining colour polymorphism in the common barn owl, a widespread nocturnal raptor species, at different scales and under different environmental conditions. I studied resource selection using GPS tracking data of breeding barn owls in Switzerland (chapters 1 and 2), as well as their behavioural response to varying local environmental conditions in relation to their plumage colouration (chapters 3 and 4). In parallel, we used skins collected in museums to investigate the evolution of plumage colouration at a worldwide scale (chapters 5 and 6). The main results obtained in the six chapters of this thesis will be discussed in the following sections.

Barn owl resource selection

In this thesis, I provide a comprehensive breakdown of resource selection by barn owls during the reproductive season, and highlight the importance of considering different scales in such analyses to understand complex animal choices. Barn owl home ranges in western Switzerland contained mainly open habitats, with a selection for the most common types (i.e. intensive meadows and cereals), corroborating the results obtained in a previous study (Arlettaz, Krähenbühl, Almasi, Roulin, & Schaub, 2010). However, when taking into account the different behavioural modes, we showed striking differences in habitat preference and avoidance. For example, during the day, barn owls roost almost exclusively in barns and farms in settlement areas, whereas, at night, they prefer to perch in pastures, meadows and along forest edges. As a whole, the results shown here unveil the barn owl as a generalist and opportunistic raptor, with a strong adaptability that allows it to exploit a variety of open habitats in intensively exploited farmland. This is consistent with the fact that this species has adapted to live in a large variety of environments, from desert-like landscapes to rainforests.

This is the first time that barn owls have been equipped with GPS devices collecting high-frequency locations, and our results provide a basis for further, more detailed analyses. For example, we approximated vegetation growth and prey density variations in our analyses by including temporal parameters in the models, but such environmental variables may vary independently from each other. Thus, upcoming studies could investigate the interaction between the vegetation structure and the different prey abundances on barn owl resource selection patterns, or even consider the influence of weather conditions on such patterns. In the current context of environmental and climatic changes, understanding the biological processes that drive animal movement may be crucial for improving prioritization in habitat management or developing efficient conservation plans (Roever et al., 2014; Suraci et al., 2019).

I was also able to appropriately evaluate the use of rare and scattered habitat types, such as the agri-environment schemes (AES) implemented in Swiss farmland to maintain and promote biodiversity. Specifically, our results showed that barn owls prefer to hunt in extensive meadows and wildflower strips, the two main AES types present in the study area. In addition, we found that males breeding in high-quality habitats – with high proportion of AES – have a higher reproductive success, without prejudicing their future breeding opportunities. This highlights the direct profitability of AES for a raptor species at the top of the food chain, complementing their already documented positive effects on plant, insect and small mammal density and species richness (e.g. Kleijn et al. 2006; Knop et al. 2006; Zingg et al. 2019). This is the first time a study highlighted the selection of AES by farmland raptors, providing support to the use of such areas to restore functional trophic chains in farmland. The combination of a high GPS location sampling rate and the use of step-selection function (Thurfjell, Ciuti, & Boyce, 2014), was key to detect the use of such rare landscape elements that previous studies could not (Arlettaz et al., 2010; Aschwanden, Birrer, & Jenni, 2005). However, these areas are rare and scattered in the landscape, and further studies should focus on the effects of the connectivity between them on their attractiveness for barn owls.

It is also particularly interesting to note how barn owls use the urban environment. Despite the apparent availability of natural roosting sites, less than 1% of roosting events (6 out of 915) took place in forests or isolated trees, which makes it an extremely rare behaviour. By observing the tracks of the approximately 500 barn owls equipped with GPS during the 5 years of this thesis, although we discovered new breeding sites outside of our nest boxes, they too were all located in barns rather than in natural settings. This all points to the strong link between barn owls and urbanized areas, probably deriving benefits such as shelter against adverse weather conditions or a reduced risk of predation, competition or harassment (Blair, 2004; Lausen & Barclay, 2006).

Alternatively, we found that barn owls avoided settlement areas when hunting, and must therefore travel several hundreds of meters – up to several kilometres – to find suitable foraging grounds. GPS data showed that barn owl males flew on average 28 km per night to feed their nestlings, with some males even covering 70 km in a single night. As barn owls soar very rarely, and only for short periods of time (Kim Schalcher, unpublished data), covering such distances probably represents a high energy cost for the parents. Although this cost is difficult to properly assess, it appears particularly clear in males that breed in low quality habitats, who have to cover larger distances each night and yet sustain lower feeding rates, translating into a reduced breeding success. Thus, although urban areas may provide some advantages as nesting sites, the associated flying energetic cost for the parents may sometimes result in reduced reproductive success. In addition, the renovation of old buildings and the spread of artificial lighting in cities are potential factors that could negatively impact the reproduction of barn owls in urban areas. In other countries, nest boxes are sometimes installed directly in the middle of the fields (Charter et al., 2012; Meyrom et al., 2009), and it would be interesting to propose such nesting opportunities in Switzerland in order to measure their attractiveness and related breeding success.

Moon illumination and barn owl colouration

We provide evidence that colouration plays an important role for nocturnal life, and that moon illumination might be involved in the evolution and maintenance of colour polymorphism of nocturnal animals. Overall, we found that reddish owls don’t fare as well as white ones in moonlit nights, being less effective at hunting and rearing their nestlings. In contrast, white owls benefit from well illuminated night and adapt their behaviour to better exploit these conditions by changing their foraging patterns. Indeed, they focus on more open habitats, in which their main prey, *M. arvalis,* occurs. In addition, white owls appear to have an advantage at capturing this prey species by inducing longer freezing responses which might consequently facilitate their capture. This suggests that white barn owls exploit sensory biases of their prey which might compensate the higher detectability of owls in general in moonlit conditions, and explain why white owls capture this type of prey more often than red ones. As a consequence, we expected white individuals to spend more time foraging on the wing in full moon conditions to exploit this advantage, however their hunting strategy (i.e. on the wing or perching) does not change with night light conditions. Thus, it remains uncertain whether white barn owls deliberately adapt their foraging strategies according to night illumination, or simply follow the prey that is more sensitive to their whiteness in moonlit nights.

Hence, our results are consistent with the background matching hypothesis (Endler, 1981; Merilaita, Scott-Samuel, & Cuthill, 2017), with white owls being less conspicuous on a clear and moonlit sky and red reddish ones being more cryptic in dark habitats (as shown in other species, see Rohwer 1990; Tate et al. 2016). Disentangling the roles of predator and prey that provide a fitness advantage to white owls in moonlit nights is not simple as it involves the interaction of four different factors: moon illumination, habitat type, prey species and colouration of the owl. Future studies could approach this issue in two ways. First, using GPS tracking data, search for fine-scale behavioural adaptations associated with night illumination, for example, if white barn owls orient themselves to face the moon when hunting to make their plumage more brilliant and exploit rodent's known aversion to light (Bourin, Petit-Demoulière, Nic Dhonnchadha, & Hascöet, 2007; Lockard, 1963). Second, to build upon our first experiment, the escape response of the different prey species should be measured under experimental conditions, by exposing them to differently coloured flying or perching owls, under various ambient light levels and with light or dark backgrounds.

Given the benefits associated with white plumage colouration revealed in this thesis, we would expect red owls to be rare in the population. However, this is not the case, suggesting that other selective pressures might favour red owls over white ones, such as a better camouflage during the day or a structural advantage of feathers containing melanin (i.e. against abrasion or thermal insulation). This is supported by the observation that female barn owls, which are much less involved in hunting than males (Roulin, 2004a), display on average redder plumages than males (A. Dreiss & Roulin, 2010; Roulin & Jensen, 2015). Selective agents acting on plumage colouration might differ between sexes according to their roles and needs, and the moon illumination seems to be one that plays a role in the hunting success of males.

A technical difficulty when measuring the impact of moon illumination on nocturnal animals, is how to properly estimate it. Different parameters could be included in the calculation of night illumination, and most studies consider the moon illuminated fraction (i.e. the percentage of the moon illuminated) as a good proxy (Penteriani, Delgado, Campioni, & Lourenço, 2010; San-Jose et al., 2019). Recently, Kyba et al. (2020) argued that the moon illuminated fraction was a poor estimator of moonlight exposure and stressed the importance of including the moon elevation over the horizon in the calculation (termed "predicted horizontal illuminance" in their article). In addition, moon illumination can be mitigated by weather conditions, and Pajot et al. (2021) proposed a formula to also account for the effect of cloud cover. Here, we estimated the moon illumination using the three approaches described above and compared it with the night luminance measured on the ground at a meteorological station in the center of the study area. Interestingly, we found that considering the moon elevation above the horizon improved strongly the approximation of the prediction of moon illuminance, whereas the inclusion of the cloud cover was not a good predictor. Although the cloudiness probably plays an important role in the nocturnal illumination, the total cloud cover data resolution used here (approx. 25 x 25 km grid) was probably too broad to properly match the light variations measured on the ground. As it is unlikely that sufficiently precise cloud cover data can be obtained in a near future, coupling light loggers to GPS tags for measuring ambient light conditions faced by the owls might be the most adequate and precise solution. Such light loggers have been shown to effectively detect nocturnal light variations (De Jong, Ouyang, Van Grunsven, Visser, & Spoelstra, 2016; Dominoni, Partecke, & Partecke, 2015), and would also allow to measure the impact of artificial lights on barn owl movements, which may be a growing issue for this nocturnal predator breeding in urbanized areas.

Convergent evolution of plumage colouration

Barn owls from three different distinct evolutionary lineages – the Afro-European *Tyto alba*, the Australasian *T. javanica* and the American *T. furcata* – have independently evolved reddish plumage morphs, with clinal distributions seen in many continents and subcontinents. As barn owl's plumage colouration is genetically determined with high heritability (h^2=0.81) (Roulin & Dijkstra, 2003; San-Jose et al., 2017), and thus weakly influenced by environmental conditions, it suggests that selective mechanisms may explain the maintenance of this polymorphism. Indeed, in Europe at least, the clinal colour variation has been shown to be locally adaptive (Antoniazza et al., 2010). Here, we found that darker barn owl morphs are associated to regions of higher annual rainfall, indicating that different plumage colouration may present specific selective advantages under various rainfall conditions. This is consistent with the Gloger's rule (Gloger, 1833), which postulates that individuals living in humid areas should be darker in colour than those living in dryer ones. The main underlying mechanism hypothesized behind this rule is linked to camouflage capabilities, with darker individuals being less conspicuous in environments with low light levels and dense vegetation. In the barn owl, this could be translated as camouflage during the day against predators and competitors, but also as being more or less cryptic when hunting at night depending on the sky conditions (see above). However, there are alternative explanations, such as that melanic traits offer better resistance to parasites, which are more numerous in humid regions, or also that melanin provides a better resistance of the feather to harsh environmental conditions. Consequently, on the basis of our results, we are not able to disentangle whether reddish plumage is a phenotypic adaptation to rainfall itself, or is associated with correlated environmental variables, such as night illumination. In this context, it is also interesting to mention that, in Switzerland, whitish owls foraged more in open areas when the sky was clear, whereas red owls foraged more along forest areas, suggesting that the pattern observed at the world scale might also occur at finer scales.

The plumage of Afro-European and American barn owls was also darker in colder regions, suggesting that reddish individuals are better adapted to cooler conditions than white ones. The Australasian taxon showed no association with temperature, although this is likely due to its smaller and homogenous range. The relation of plumage colour with temperature is consistent with another major evolutionary rule, Bogert's rule (Bogert, 1949), which predicts that dark individuals have a selective advantage in cold regions as they absorb better solar radiations, and thus heat up faster than paler individuals. Although we cannot completely exclude it, a thermoregulatory advantage related to solar radiation seems unlikely in a nocturnal animal. It appears more plausible that melanin may directly improve the thermic insulation of the feather (i.e. structural differences), or indirectly by being associated to specific physiological functions. Indeed, melanin is produced by the melanocortin system which also regulates, among others, behavioural and immunity traits that may be the primary target of selection (Almasi, Jenni, Jenni-Eiermann, & Roulin, 2010; Ducrest, Keller, & Roulin, 2008).

In addition to the effects of climatic conditions on barn owl colouration, we found that white barn owls preyed on bigger species than reddish ones. This suggests that predator-prey interactions at the world scale might also contribute to the maintenance of colour polymorphism in this species. However, the correlative nature of the present studies renders the interconnection between habitat characteristics, climatic conditions and the type of prey difficult to disentangle, and stresses the need for experimental research testing specifically the hypotheses emitted above. Finally, although the mechanism behind these results is still unclear, the recurrent association between plumage colouration and rainfall, temperature and prey seen in the different barn owl lineages is strong evidence that natural selection is responsible for the convergent evolution of plumage colouration on different continents.

Conclusion

In this thesis, I illustrate how multi-scale analyses provide a wealth of opportunities to study the ecology and evolution of organisms from numerous perspectives. Having a widespread distribution and displaying easily measurable phenotypic variation, the barn owl offers a particularly appropriate system for tackling both applied and fundamental research questions. First, I was able to address applied conservation issues by studying at high resolution how this species exploits its habitat in Swiss farmland. On top of providing a comprehensive breakdown of resource selection by barn owls during the reproductive season, I highlighted the importance of considering different scales in analysing complex animal movements. Second, I was also able to tackle more fundamental subjects, namely the evolution and maintenance of colour polymorphism, both at local and worldwide scales. I showed that climatic conditions, moon illumination, habitat features and prey all contribute to explaining the variations in plumage colouration of the barn owl at different scales. Finally, this thesis provides strong evidence that plumage colouration repeatedly evolved under natural selection in the different barn owl lineages.

Publication List

1. Dreiss, A. N., **Séchaud, R.**, Béziers, P., Villain, N., Genoud, M., Almasi, B., … Roulin, A. (2016). Social huddling and physiological thermoregulation are related to melanism in the nocturnal barn owl. Oecologia, 180(2), 371–381. https://doi.org/10.1007/s00442-015-3491-3
2. Romano, A., **Séchaud, R.**, Hirzel, A. H., & Roulin, A. (2019). Climate-driven convergent evolution of plumage colour in a cosmopolitan bird. Global Ecology and Biogeography, 28(4), 496–507. https://doi.org/10.1111/geb.12870
3. San-Jose, L. M., **Séchaud, R.**, Schalcher, K., Judes, C., Questiaux, A., Oliveira-Xavier, A., … Roulin, A. (2019). Differential fitness effects of moonlight on plumage colour morphs in barn owls. Nature Ecology and Evolution, 3(9), 1331–1340. https://doi.org/10.1038/s41559-019-0967-2
4. **Séchaud, R.**, Machado, A. P., Schalcher, K., Simon, C., & Roulin, A. (2019). Communally breeding female Barn Owls *Tyto alba* are not related and do not invest similarly in the communal family. Bird Study, 66(4), 570–573. https://doi.org/10.1080/00063657.2020.1732291
5. Romano, A., **Séchaud, R.**, & Roulin, A. (2020). Geographical variation in bill size provides evidence for Allen's rule in a cosmopolitan raptor. Global Ecology and Biogeography, 29(1), 65–75. https://doi.org/10.1111/geb.13007
6. Romano, A., **Séchaud, R.**, & Roulin, A. (2020). Global biogeographical patterns in the diet of a cosmopolitan avian predator. Journal of Biogeography, 47(7), 1467–1481. https://doi.org/10.1111/jbi.13829
7. Fleming, C. H., Drescher-Lehman, J., Noonan, M. J., Akre, T. S. B., Brown, D. J., Cochrane, M. M., … Calabrese, J. M. (2020). A comprehensive framework for handling location error in animal tracking data. BioRxiv, 31. https://doi.org/10.1101/2020.06.12.130195
8. Romano, A., **Séchaud, R.**, & Roulin, A. (2021). Evolution of wing length and melanin-based coloration in insular populations of a cosmopolitan raptor. Journal of Biogeography, 48(4), 961–973. https://doi.org/10.1111/jbi.14053
9. Romano, A., **Séchaud, R.**, & Roulin, A. (2021). Generalized evidence for Bergmann's rule: body size variation in a cosmopolitan owl genus. Journal of Biogeography, 48(1), 51–63. https://doi.org/10.1111/jbi.13981
10. Romano, A., **Séchaud, R.**, & Roulin, A. (2021). Geographic variation in body size and plumage colour according to diet composition in a nocturnal raptor. Journal of Avian Biology. https://doi.org/10.1111/jav.02716
11. Cosandey, V., **Séchaud, R.**, Béziers, P., Chittaro, Y., Sanchez, A., & Roulin, A. (2021). Nidicolous beetle species richness is driven by Barn Owl's nests occupancy and landscape structure. Journal of Ornithology, 1, 3. https://doi.org/10.1007/s10336-021-01875-z
12. **Séchaud, R.**, Schalcher, K., Machado, A. P., Almasi, B., Massa, C., Safi, K., & Roulin, A. (2021). Behaviour-specific habitat selection patterns of breeding barn owls. Movement Ecology, 9(1), 18. https://doi.org/10.1186/s40462-021-00258-6

References

Åbjörnsson, K., Hansson, L. A., & Brönmark, C. (2004). Responses of prey from habitats with different predator regimes: Local adaptation and heritability. *Ecology*, *85*(7), 1859–1866. https://doi.org/10.1890/03-0074

Ahnesjö, J., & Forsman, A. (2006). Differential habitat selection by pygmy grasshopper color morphs; interactive effects of temperature and predator avoidance. *Evolutionary Ecology*, *20*(3), 235–257. https://doi.org/10.1007/s10682-006-6178-8

Aliabadian, M., Alaei-Kakhki, N., Mirshamsi, O., Nijman, V., & Roulin, A. (2016). Phylogeny, biogeography, and diversification of barn owls (Aves: Strigiformes). *Biological Journal of the Linnean Society*, *119*(4), 904–918. https://doi.org/10.1111/bij.12824

Allen, A. M., & Singh, N. J. (2016). Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, *3*(JAN), 155. https://doi.org/10.3389/fevo.2015.00155

Allen, J. A. (1988). Frequency-dependent selection by predators. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *319*(1196), 485–503. https://doi.org/10.1098/rstb.1988.0061

Almasi, B., Jenni, L., Jenni-Eiermann, S., & Roulin, A. (2010). Regulation of stress response is heritable and functionally linked to melanin-based coloration. *Journal of Evolutionary Biology*, *23*(5), 987–996. https://doi.org/10.1111/j.1420-9101.2010.01969.x

Antoniazza, S., Burri, R., Fumagalli, L., Goudet, J., & Roulin, A. (2010). Local adaptation maintains clinal variation in melanin-based coloration of European barn owls (*Tyto alba*). *Evolution*, *64*(7), 1944–1954. https://doi.org/10.1111/j.1558-5646.2010.00969.x

Antoniazza, S., Kanitz, R., Neuenschwander, S., Burri, R., Gaigher, A., Roulin, A., & Goudet, J. (2014). Natural selection in a postglacial range expansion: the case of the colour cline in the European barn owl. *Molecular Ecology*, *23*, 5508–5523. https://doi.org/10.1111/mec.12957

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. *Journal of Ornithology*, *151*(3), 553–564. https://doi.org/10.1007/s10336-009-0485-0

Armbruster, W. S. (2002). Can indirect selection and genetic context contribute to trait diversification? A transition-probability study of blossom-colour evolution in two genera.

Journal of Evolutionary Biology, *15*(3), 468–486. https://doi.org/10.1046/j.1420-9101.2002.00399.x

Aschwanden, J., Birrer, S., & Jenni, L. (2005). Are ecological compensation areas attractive hunting sites for common kestrels (*Falco tinnuculus*) and long-eared owls (*Asio otus*)? *Journal of Ornithology*, *146*(3), 279–286. https://doi.org/10.1007/s10336-005-0090-9

Ausprey, I. J., & Rodewald, A. D. (2011). Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. *Auk*, *128*(2), 293–302. https://doi.org/10.1525/auk.2011.10158

Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology*, *229*(2), 209–220. https://doi.org/10.1016/j.jtbi.2004.03.016

Bergin, T. M. (1992). Habitat Selection by the Western Kingbird in Western Nebraska: A Hierarchical Analysis. *The Condor*, *94*(4), 903–911. https://doi.org/10.2307/1369287

Bergmann, C. (1847). *Über die Verhältnisse der Wärmeökonomie der Thiere* (1st ed.).

Blair, R. (2004). The Effects of Urban Sprawl on Birds at Multiple Levels of Biological Organization. *Ecology and Society*, *9*(5).

Bogert, C. M. (1949). Thermoregulation in Reptiles, A Factor in Evolution. *Evolution*, *3*(3), 195. https://doi.org/10.2307/2405558

Bond, A. B., & Kamil, A. C. (1998). Apostatic selection by blue jays produces balanced polymorphism in virtual prey. *Nature*, *395*(6702), 594–596. https://doi.org/10.1038/26961

Bourin, M., Petit-Demoulière, B., Nic Dhonnchadha, B., & Hascöet, M. (2007). Animal models of anxiety in mice. *Fundamental and Clinical Pharmacology*, *21*(6), 567–574. https://doi.org/10.1111/j.1472-8206.2007.00526.x

Bowyer, R. T., & Kie, J. G. (2006). Effects of scale on interpreting life-history characteristics of ungulates and carnivores. *Diversity and Distributions*, *12*(3), 244–257. https://doi.org/10.1111/j.1366-9516.2006.00247.x

Boyce, M. S. (2006). Scale for resource selection functions. *Diversity and Distributions*, *12*(3), 269–276. https://doi.org/10.1111/j.1366-9516.2006.00243.x

Bozek, C. K., Prange, S., & Gehrt, S. D. (2007). The influence of anthropogenic resources on multi-scale habitat selection by raccoons. *Urban Ecosystems*, *10*(4), 413–425. https://doi.org/10.1007/s11252-007-0033-8

Bradshaw, A. D. (1960). Population differentiation in *Agrostis Tenuis Sibth*: Populations in varied environments. *New Phytologist*, *59*(1), 92–103. https://doi.org/10.1111/j.1469-8137.1960.tb06206.x

Brown, B. A., & Clegg, M. T. (1984). Influence of Flower Color Polymorphism on Genetic Transmission in a Natural Population of the Common Morning Glory, *Ipomoea purpurea*. *Evolution*, *38*(4), 796–803.

Chappell, M. A., & Snyder, L. R. (1984). Biochemical and physiological correlates of deer mouse alpha-chain hemoglobin polymorphisms. *Proceedings of the National Academy of Sciences of the United States of America*, *81*(17), 5484–5488. https://doi.org/10.1073/pnas.81.17.5484

Charter, M., Leshem, Y., Meyrom, K., Peleg, O., & Roulin, A. (2012). The importance of micro-habitat in the breeding of Barn Owls *Tyto alba*. *Bird Study*, *59*(3), 368–371. https://doi.org/10.1080/00063657.2012.669360

Clusella Trullas, S., van Wyk, J. H., & Spotila, J. R. (2007). Thermal melanism in ectotherms. *Journal of Thermal Biology*, *32*(5), 235–245. https://doi.org/10.1016/j.jtherbio.2007.01.013

Cochran, W. W., & Lord, R. D. (1963). A Radio-Tracking System for Wild Animals. *The Journal of Wildlife Management*, *27*(1), 9. https://doi.org/10.2307/3797775

Cody, M. L. (1981). Habitat Selection in Birds: The Roles of Vegetation Structure, Competitors, and Productivity. *BioScience*, *31*(2), 107–113. https://doi.org/10.2307/1308252

Coop, G., Witonsky, D., Di Rienzo, A., & Pritchard, J. K. (2010). Using environmental correlations to identify loci underlying local adaptation. *Genetics*, *185*(4), 1411–1423. https://doi.org/10.1534/genetics.110.114819

Cushman, S. A., & Lewis, J. S. (2010). Movement behavior explains genetic differentiation in American black bears. *Landscape Ecology*, *25*(10), 1613–1625. https://doi.org/10.1007/s10980-010-9534-6

Darwin, C. (1859). *On the origin of species by means of natural selection*. (J. Murray, Ed.). London.

Daversa, D. R., Fenton, A., Dell, A. I., Garner, T. W. J., & Manica, A. (2017). Infections on the move: How transient phases of host movement influence disease spread. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1869). https://doi.org/10.1098/rspb.2017.1807

Davis, W. E., Jackson, J. A., & Tautin, J. (2008). Bird banding in North Amercia: the first hundred years. *Memoirs of the Nuttall Ornithological Club*, *15*, 220–229.

De Jong, M., Ouyang, J. Q., Van Grunsven, R. H. A., Visser, M. E., & Spoelstra, K. (2016). Do wild great tits avoid exposure to light at night? *PLoS ONE*, *11*(6), e0157357. https://doi.org/10.1371/journal.pone.0157357

DeCesare, N. J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L., & Musiani, M. (2014). Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology*, *83*(2), 343–352. https://doi.org/10.1111/1365-2656.12144

Dominoni, D. M., Partecke, J., & Partecke, J. (2015). Does light pollution alter daylength? A test using light loggers on free-ranging european blackbirds (*turdus merula*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1667). https://doi.org/10.1098/rstb.2014.0118

Dong, Y. wei, Li, X. X., Choi, F. M. P., Williams, G. A., Somero, G. N., & Helmuth, B. (2017). Untangling the roles of microclimate, behaviour and physiological polymorphism in governing vulnerability of intertidal snails to heat stress. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1854). https://doi.org/10.1098/rspb.2016.2367

Dreiss, A., Antoniazza, S., Burri, R., Fumagalli, L., Sonnay, C., Frey, C., … Roulin, A. (2012). Local adaptation and matching habitat choice in female barn owls with respect to melanic coloration. *Journal of Evolutionary Biology*, *25*(1), 103–114. https://doi.org/10.1111/j.1420-9101.2011.02407.x

Dreiss, A. N., Séchaud, R., Béziers, P., Villain, N., Genoud, M., Almasi, B., … Roulin, A. (2016). Social huddling and physiological thermoregulation are related to melanism in the nocturnal barn owl. *Oecologia*, *180*(2), 371–381. https://doi.org/10.1007/s00442-015-3491-3

Dreiss, A., & 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*(3), 689–704. https://doi.org/10.1111/j.1095-8312.2010.01503.x

Ducrest, A.-L., Keller, L., & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution*, *23*(9), 502–510. https://doi.org/10.1016/j.tree.2008.06.001

Dussault, C., Quellet, J. P., Courtois, R., Huot, J., Breton, L., & Jolicoeur, H. (2005). Linking moose habitat selection to limiting factors. *Ecography*, *28*(5), 619–628. https://doi.org/10.1111/j.2005.0906-7590.04263.x

Endler, J. A. (1981). An overview of the relationships between mimicry and crypsis. *Biological Journal* *of the Linnean Society*, *16*(1), 25–31. https://doi.org/10.1111/j.1095-8312.1981.tb01840.x

Fauchald, P., & Tveraa, T. (2003). Using fisrt-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, *84*(2), 282–288. https://doi.org/10.1890/0012-9658(2003)084[0282:UFPTIT]2.0.CO;2

Ford, E. B. (1945). Polymorphism. *Biological Reviews*, *20*(2), 73–88. https://doi.org/10.1111/j.1469-185X.1945.tb00315.x

Forsman, A. (2016). Is colour polymorphism advantageous to populations and species? *Molecular Ecology*, *25*(12), 2693–2698. https://doi.org/10.1111/mec.13629

Fraser, K. C., Davies, K. T. A., Davy, C. M., Ford, A. T., Flockhart, D. T. T., & Martins, E. G. (2018). Tracking the conservation promise of movement ecology. *Frontiers in Ecology and Evolution*, *6*(OCT), 150. https://doi.org/10.3389/fevo.2018.00150

Galeotti, P., Rubolini, D., Dunn, P. O., & Fasola, M. (2003). Colour polymorphism in birds: causes and functions. *Journal of Evolutionary Biology*, *16*(4), 635–646. https://doi.org/10.1046/j.1420-9101.2003.00569.x

Garriga, J., Palmer, J. R. B., Oltra, A., & Bartumeus, F. (2016). Expectation-Maximization Binary Clustering for Behavioural Annotation. *PLOS ONE*, *11*(3), e0151984. https://doi.org/10.1371/journal.pone.0151984

Gavrilets, S. (2003). Perspective: Models of speciation - What have we learned in 40 years? *Evolution*, *57*(10), 2197–2215. https://doi.org/10.1111/j.0014-3820.2003.tb00233.x

Gibbons, W. J., & Andrews, K. M. (2004). PIT Tagging: Simple Technology at Its Best. *BioScience*, *54*(5), 66–74. https://doi.org/10.1641/0006-3568(2004)054

Gloger, C. L. (1833). *Das Abändern der Vögel durch Einfluss des Klima's*. *Breslau*.

Gould, B., McCouch, S., & Geber, M. (2014). Variation in soil aluminium tolerance genes is associated with local adaptation to soils at the Park Grass Experiment. *Molecular Ecology*, *23*(24), 6058–6072. https://doi.org/10.1111/mec.12893

Greco, C. F., & Kevan, P. G. (1999). Polyethism in foraging in a polymorphic predator, *Enoplognatha ovata* (Araneae: Theridhdae): A case for balance. *Canadian Entomologist*, *131*(2), 259–268. https://doi.org/10.4039/ent131259-2

Greischar, M. A., & Koskella, B. (2007). A synthesis of experimental work on parasite local adaptation. *Ecology Letters*, *10*(5), 418–434. https://doi.org/10.1111/j.1461-0248.2007.01028.x

Grøndahl, E., & Ehlers, B. K. (2008). Local adaptation to biotic factors: Reciprocal transplants of four species associated with aromatic *Thymus pulegioides* and *T. serpyllum*. *Journal of Ecology*, *96*(5), 981–992. https://doi.org/10.1111/j.1365-2745.2008.01407.x

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat Suitability and Distribution Models: with Applications in R* (1st ed., Vol. 1). Cambridge University Press.

Hanski, I., Kuussaari, M., & Nieminen, M. (1994). Metapopulation structure and migration in the butterfly Melitaea cinxia. *Ecology*, *75*(3), 747–762. https://doi.org/10.2307/1941732

Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist*, *173*(5), 579–588. https://doi.org/10.1086/597611

Hetem, R. S., de Witt, B. A., Fick, L. G., Fuller, A., Kerley, G. I. H., Meyer, L. C. R., … Maloney, S. K. (2009). Body temperature, thermoregulatory behaviour and pelt characteristics of three colour morphs of springbok (*Antidorcas marsupialis*). *Comparative Biochemistry and Physiology, Part A*, *152*(3), 379–388. https://doi.org/10.1016/j.cbpa.2008.11.011

Hill, G. E., & McGraw, K. J. (2006). *Bird Coloration: Mechanisms and Measurements* (Vol. 1). Harvard University Press.

Hoeksema, J. D., & Forde, S. E. (2008). A meta-analysis of factors affecting local adaptation between interacting species. *American Naturalist*, *171*(3), 275–290. https://doi.org/10.1086/527496

Hoekstra, H. E., Krenz, J. G., & Nachman, M. W. (2005). Local adaptation in the rock pocket mouse (*Chaetodipus intermedius*): Natural selection and phylogenetic history of populations. *Heredity*, *94*(2), 217–228. https://doi.org/10.1038/sj.hdy.6800600

Hoffman, E. A., & Blouin, M. S. (2000). A review of colour and pattern polymorphisms in anurans. *Biological Journal of the Linnean Society*, *70*(4), 633–665. https://doi.org/10.1006/bijl.1999.0421

Hoffman, J. I., Bauer, E., Paijmans, A. J., Humble, E., Beckmann, L. M., Kubetschek, C., … Lowther, A. (2018). A global cline in a colour polymorphism suggests a limited contribution of gene flow towards the recovery of a heavily exploited marine mammal. *Royal Society Open Science*, *5*(10). https://doi.org/10.1098/rsos.181227

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., & Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19060–19065.

Hughes, J. J., Ward, D., & Perrin, M. R. (1994). Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology*, *75*(5), 1397–1405. https://doi.org/10.2307/1937463

Hugie, D. M., & Dill, L. M. (1994). Fish and game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology*, *45*, 151–169. https://doi.org/10.1111/j.1095-8649.1994.tb01090.x

Huxley, J. (1955). Morphism and evolution. *Heredity*, *9*(1), 1–52. https://doi.org/10.1038/hdy.1955.1

Jain, S. K., & Bradshaw, A. D. (1966). Evolutionary divergence among adjacent plant populations I. The evidence and its theoretical analysis. *Heredity*, *21*(3), 407–441. https://doi.org/10.1038/hdy.1966.42

Jefferies, R. L., Jano, A. P., & Abraham, K. F. (2006). A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, *94*(1), 234–242. https://doi.org/10.1111/j.1365-2745.2005.01086.x

Jeltsch, F., Bonte, D., Pe’er, G., Reineking, B., Leimgruber, P., Balkenhol, N., … Bauer, S. (2013). Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology*, *1*(1), 1–13. https://doi.org/10.1186/2051-3933-1-6

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, *61*(1), 65–71. https://doi.org/10.2307/1937156

Jordan, F., Bartolini, M., Nelson, C., Patterson, P. E., & Soulen, H. L. (1997). Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, *208*(1–2), 45–56. https://doi.org/10.1016/S0022-0981(96)02656-1

Kaltz, O., & Shykoff, J. A. (1998). Local adaptation in host–parasite systems. *Heredity*, *81*(4), 361–370. https://doi.org/10.1046/j.1365-2540.1998.00435.x

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, *7*(12), 1225–1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240). https://doi.org/10.1126/science.aaa2478

Kettlewell, H. B. D. (1955). Selection experiments on industrial melanism in the Lepidoptera. *Heredity*, *9*(3), 323–342. https://doi.org/10.1038/hdy.1955.36

Kettlewell, H. B. D. (1956). Further selection experiments on industrial melanism in the Lepidoptera.

Heredity, *10*(3), 287–301. https://doi.org/10.1038/hdy.1956.28

Kim, E., & Donohue, K. (2013). Local adaptation and plasticity of *Erysimum capitatum* to altitude: Its implications for responses to climate change. *Journal of Ecology*, *101*(3), 796–805. https://doi.org/10.1111/1365-2745.12077

Kirkpatrick, M., & Barton, N. (2006). Chromosome inversions, local adaptation and speciation. *Genetics*, *173*(1), 419–434. https://doi.org/10.1534/genetics.105.047985

Kirkpatrick, M., & Barton, N. H. (1997). Evolution of a species' range. *American Naturalist*, *150*(1), 1–23. https://doi.org/10.1086/286054

Kleijn, D., Baquero, R. A., Clough, Y., Díaz, M., Esteban, J., Fernández, F., … Yela, J. L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, *9*(3), 243–254. https://doi.org/10.1111/j.1461-0248.2005.00869.x

Klinka, D. R., & Reimchen, T. E. (2009). Adaptive coat colour polymorphism in the Kermode bear of coastal British Columbia. *Biological Journal of the Linnean Society*, *98*(3), 479–488. https://doi.org/10.1111/j.1095-8312.2009.01306.x

Knop, E., Kleijn, D., Herzog, F., & Schmid, B. (2006). Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology*, *43*(1), 120–127. https://doi.org/10.1111/j.1365-2664.2005.01113.x

Kyba, C. C. M., Conrad, J., & Shatwell, T. (2020). Lunar illuminated fraction is a poor proxy for moonlight exposure. *Nature Ecology and Evolution*, *4*(3), 318–319. https://doi.org/10.1038/s41559-020-1096-7

Lank, D. B., Smith, C. M., Hanotte, O., Burke, T., & Cooke, F. (1995). Genetic polymorphism for alternative mating behaviour in lekking male ruff *philomachus pugnax*. *Nature*, *378*(6552), 59–62. https://doi.org/10.1038/378059a0

Lausen, C. L., & Barclay, R. M. R. (2006). Benefits of living in a building: Big brown bats (*Eptesicus fuscus*) in rocks versus buildings. *Journal of Mammalogy*, *87*(2), 362–370. https://doi.org/10.1644/05-MAMM-A-127R1.1

Levene, H. (1953). Genetic Equilibrium When More Than One Ecological Niche is Available. *The American Naturalist*, *87*(836), 331–333. https://doi.org/10.1086/281792

Levins, R. (1979). Coexistence in a Variable Environment. *The American Naturalist*, *114*(6), 765–783. https://doi.org/10.1086/283527

Lockard, R. B. (1963). Some effects of light upon the behavior of rodents. *Psychological Bulletin*, *60*(6), 509–529. https://doi.org/10.1037/h0046113

Lonsdale, D. J., & Levinton, J. S. (1985). Latitudinal differentiation in copepod growth: an adaptation to temperature. *Ecology*, *66*(5), 1397–1407. https://doi.org/10.2307/1938002

Losey, J. E., Ives, A. R., Harmon, J., Ballantyne, F., & Brown, C. (1997). A polymorphism maintained by opposite patterns of parasitism and predation. *Nature*, *388*(6639), 269–272. https://doi.org/10.1038/40849

Macdonald, D. W., Bothwell, H. M., Hearn, A. J., Cheyne, S. M., Haidir, I., Hunter, L. T. B., … Cushman, S. A. (2018). Multi-scale habitat selection modeling identifies threats and conservation opportunities for the Sunda clouded leopard (*Neofelis diardi*). *Biological Conservation*, *227*, 92–103. https://doi.org/10.1016/j.biocon.2018.08.027

Majerus, M. E. N., Brunton, C. F. A., & Stalker, J. (2000). A bird's eye view of the peppered moth. *Journal of Evolutionary Biology*, *13*(2), 155–159. https://doi.org/10.1046/j.1420-9101.2000.00170.x

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals : statistical design and analysis for field studies*. Kluwer Academic Publishers.

Mather, K. (1955). Polymorphism as an Outcome of Disruptive Selection. *Evolution*, *9*(1), 52. https://doi.org/10.2307/2405357

Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat Selection at Multiple Scales. *Ecoscience*, *16*(2), 238–247. Retrieved from https://pubag.nal.usda.gov/pubag/article.xhtml?id=1267421

Mayr, E. (1963). *Animal Species and Evolution*. *Harvard University Press*.

McCollin, D. (1998). Forest edges and habitat selection in birds: A functional approach. *Ecography*, *21*(3), 247–260. https://doi.org/10.1111/j.1600-0587.1998.tb00562.x

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology*, *31*(6), 1161–1175. https://doi.org/10.1007/s10980-016-0374-x

McKay, J. K., Bishop, J. G., Lin, J. Z., Richards, J. H., Sala, A., & Mitchell-Olds, T. (2001). Local adaptation across a climatic gradient despite small effective population size in the rare sapphire rockcress. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1477), 1715–1721.

https://doi.org/10.1098/rspb.2001.1715

McKinnon, J. S., & Pierotti, M. E. R. (2010). Colour polymorphism and correlated characters: Genetic mechanisms and evolution. *Molecular Ecology*, *19*(23), 5101–5125. https://doi.org/10.1111/j.1365-294X.2010.04846.x

Meiri, S. (2011). Bergmann's Rule - what's in a name? *Global Ecology and Biogeography*, *20*(1), 203–207. https://doi.org/10.1111/j.1466-8238.2010.00577.x

Merilaita, S., Scott-Samuel, N. E., & Cuthill, I. C. (2017). How camouflage works. *Philosophical Transactions of the Royal Society B: Biological Sciences*. Royal Society. https://doi.org/10.1098/rstb.2016.0341

Meyrom, K., Motro, Y., Leshem, Y., Aviel, S., Izhaki, I., Argyle, F., & Charter, M. (2009). Nest-Box use by the Barn Owl *Tyto alba* in a Biological Pest Control Program in the Beit She'an Valley, Israel. *Ardea*, *97*(4), 463–467. https://doi.org/10.5253/078.097.0410

Morris, D. W. (2003). Toward an ecological synthesis: a case for habitat selection. *Oecologia*, *136*, 1–13. https://doi.org/10.1007/s00442-003-1241-4

Muir, A. P., Biek, R., Thomas, R., & Mable, B. K. (2014). Local adaptation with high gene flow: Temperature parameters drive adaptation to altitude in the common frog (*Rana temporaria*). *Molecular Ecology*, *23*(3), 561–574. https://doi.org/10.1111/mec.12624

Mullen, L. M., & Hoekstra, H. E. (2008). Natural selection along an environmental gradient: A classic cline in mouse pigmentation. *Evolution*, *62*(7), 1555–1570. https://doi.org/10.1111/j.1558-5646.2008.00425.x

Muri, D., Schuerch, J., Trim, N., Golay, J., Baillifard, A., El Taher, A., & Dubey, S. (2015). Thermoregulation and microhabitat choice in the polymorphic asp viper (*Vipera aspis*). *Journal of Thermal Biology*, *53*, 107–112. https://doi.org/10.1016/j.jtherbio.2015.06.009

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19052–19059. https://doi.org/10.1073/pnas.0800375105

Orians, G. H., & Wittenberger, J. F. (1991). Spatial and temporal scales in habitat selection. *American Naturalist*, *137*. https://doi.org/10.1086/285138

Pagel, J., & Schurr, F. M. (2012). Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography*, *21*(2), 293–304.

https://doi.org/10.1111/j.1466-8238.2011.00663.x

Pajot, A., Corbeau, A., Jambon, A., & Weimerskirch, H. (2021). Diel at-sea activity of two species of great albatrosses: the ontogeny of foraging and movement behaviour. *Journal of Avian Biology*, *52*(2). https://doi.org/10.1111/jav.02597

Passarotto, A., Parejo, D., Penteriani, V., & Avilés, J. M. (2018). Colour polymorphism in owls is linked to light variability. *Oecologia*, 1–13. https://doi.org/10.1007/s00442-018-4128-0

Paulson, D. R. (1973). Predator Polymorphism and Apostatic Selection. *Evolution*, *27*(2), 269. https://doi.org/10.2307/2406967

Penteriani, V., Delgado, M. del M., Campioni, L., & Lourenço, R. (2010). Moonlight Makes Owls More Chatty. *PLoS ONE*, *5*(1), e8696. https://doi.org/10.1371/journal.pone.0008696

Pryke, S. R., Astheimer, L. B., Buttemer, W. A., & Griffith, S. C. (2007). Frequency-dependent physiological trade-offs between competing colour morphs. *Biology Letters*, *3*(5), 494–497. https://doi.org/10.1098/rsbl.2007.0213

Roberts, S., Guilford, T., Rezek, I., & Biro, D. (2004). Positional entropy during pigeon homing I: application of Bayesian latent state modelling. *Journal of Theoretical Biology*, *227*(1), 39–50. https://doi.org/10.1016/J.JTBI.2003.07.002

Roever, C. L., Beyer, H. L., Chase, M. J., & van Aarde, R. J. (2014). The pitfalls of ignoring behaviour when quantifying habitat selection. *Diversity and Distributions*, *20*(3), 322–333. https://doi.org/10.1111/ddi.12164

Rohwer, S., & Paulson, D. R. (1987). The avoidance-image hypothesis and color polymorphism in Buteo hawks. *Ornis Scandinavica*, *18*(4), 285–290. https://doi.org/10.2307/3676897

Rohwer, Sievert. (1990). Foraging differences between white and dark morphs of the Pacific Reef Heron *Egretta sacra*. *Ibis*, *132*(1), 21–26. https://doi.org/10.1111/j.1474-919X.1990.tb01012.x

Rosenzweig, M. L. (1985). Some theoretical aspects of habitat selection. In *Habitat selection in birds* (pp. 517–540). Academic Press.

Rosenzweig, Michael L. (1981). A Theory of Habitat Selection. *Ecology*, *62*(2), 327–335. https://doi.org/10.2307/1936707

Roulin, A. (2003). Geographic variation in sexual dimorphism in the barn owl *Tyto alba*: a role for direct selection or genetic correlation? *Journal of Avian Biology*, *34*(3), 251–258. https://doi.org/10.1034/j.1600-048X.2003.03022.x

Roulin, A. (2004a). Covariation between plumage colour polymorphism and diet in the Barn Owl *Tyto alba*. *Ibis*, *146*(3), 509–517.

Roulin, A. (2004b). The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews*, *79*(4), 815–848. https://doi.org/10.1017/S1464793104006487

Roulin, A. (2020). *Barn Owls: Evolution and Ecology*. Cambridge University Press.

Roulin, A., & Altwegg, R. (2007). Breeding rate is associated with pheomelanism in male and with eumelanism in female barn owls. *Behavioral Ecology*, *18*(3), 563–570. https://doi.org/10.1093/beheco/arm015

Roulin, A., & Dijkstra, C. (2003). Genetic and environmental components of variation in eumelanin and phaeomelanin sex-traits in the barn owl. *Heredity*, *90*(5), 359–364.

Roulin, A., Ducret, B., Ravussin, P. A., & Altwegg, R. (2003). Female colour polymorphism covaries with reproductive strategies in the tawny owl Strix aluco. *Journal of Avian Biology*, *34*(4), 393–401. https://doi.org/10.1111/j.0908-8857.2003.03139.x

Roulin, A., & Jensen, H. (2015). Sex-linked inheritance, genetic correlations and sexual dimorphism in three melanin-based colour traits in the barn owl. *Journal of Evolutionary Biology*, *28*(3), 655–666. https://doi.org/10.1111/jeb.12596

Roulin, A., & Wink, M. (2004). Predator-prey relationships and the evolution of colour polymorphism: a comparative analysis in diurnal raptors. *Biological Journal of the Linnean Society*, *81*(4), 565–578. https://doi.org/10.1111/j.1095-8312.2004.00308.x

Rueffler, C., Van Dooren, T. J. M., Leimar, O., & Abrams, P. A. (2006). Disruptive selection and then what? *Trends in Ecology & Evolution*, *21*(5), 238–245. https://doi.org/10.1016/j.tree.2006.03.003

San-Jose, L. M., Ducrest, A. L., Ducret, V., Simon, C., Richter, H., Wakamatsu, K., & Roulin, A. (2017). MC1R variants affect the expression of melanocortin and melanogenic genes and the association between melanocortin genes and coloration. *Molecular Ecology*, *26*(1), 259–276. https://doi.org/10.1111/mec.13861

San-Jose, L. M., Séchaud, R., Schalcher, K., Judes, C., Questiaux, A., Oliveira-Xavier, A., … Roulin, A. (2019). Differential fitness effects of moonlight on plumage colour morphs in barn owls. *Nature Ecology and Evolution*, *3*(9), 1331–1340. https://doi.org/10.1038/s41559-019-0967-2

Schweiger, O., Heikkinen, R. K., Harpke, A., Hickler, T., Klotz, S., Kudrna, O., … Settele, J. (2012).

Increasing range mismatching of interacting species under global change is related to their ecological characteristics. *Global Ecology and Biogeography*, *21*(1), 88–99. https://doi.org/10.1111/j.1466-8238.2010.00607.x

Shafer, A. B. A., Northrup, J. M., White, K. S., Boyce, M. S., Côté, S. D., & Coltman, D. W. (2012). Habitat selection predicts genetic relatedness in an alpine ungulate. *Ecology*, *93*(6), 1317–1329. https://doi.org/10.1890/11-0815.1

Simpson, C., Jackson, J. B. C., & Herrera-Cubilla, A. (2017). Evolutionary determinants of morphological polymorphism in colonial animals. *American Naturalist*, *190*(1), 17–28. https://doi.org/10.1086/691789

Skulason, S., & Smith, T. B. (1995). Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution*, *10*(9), 366–370. https://doi.org/10.1016/S0169-5347(00)89135-1

Smith, T. B. (1987). Bill size polymorphism and intraspecific niche utilization in an African finch. *Nature*, *329*(6141), 717–719. https://doi.org/10.1038/329717a0

Sobel, J. M., Chen, G. F., Watt, L. R., & Schemske, D. W. (2010). The biology of speciation. *Evolution*, *64*(2), 295–315. https://doi.org/10.1111/j.1558-5646.2009.00877.x

Stapp, P., Polis, G. A., & Sánchez Piñero, F. (1999). Stable isotopes reveal strong marine and El Nino effects on island food webs. *Nature*, *401*(6752), 467–469. https://doi.org/10.1038/46769

Suraci, J. P., Frank, L. G., Oriol-Cotterill, A., Ekwanga, S., Williams, T. M., & Wilmers, C. C. (2019). Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. *Ecology*, *100*(4), e02644. https://doi.org/10.1002/ecy.2644

Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., … Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, *101*(1), 58–67. https://doi.org/10.1111/1365-2745.12025

Svensson, E. I. (2017). Back to basics: Using colour polymorphisms to study evolutionary processes. *Molecular Ecology*, *26*(8), 2204–2211. https://doi.org/10.1111/mec.14025

Tate, G. J., Bishop, J. M., & Amar, A. (2016). Differential foraging success across a light level spectrum explains the maintenance and spatial structure of colour morphs in a polymorphic bird. *Ecology Letters*, *19*(6), 679–686. https://doi.org/10.1111/ele.12606

Taylor, I. (1994). *Barn Owls: Predator-Prey Relationships and Conservation*. Cambridge University Press.

Thiebault, A., & Tremblay, Y. (2013). Splitting animal trajectories into fine-scale behaviorally consistent movement units: Breaking points relate to external stimuli in a foraging seabird. *Behavioral Ecology and Sociobiology*, *67*(6), 1013–1026. https://doi.org/10.1007/s00265-013-1546-1

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, *2*(1), 4. https://doi.org/10.1186/2051-3933-2-4

Tso, I. M., Tai, P. L., Ku, T. H., Kuo, C. H., & Yang, E. C. (2002). Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tetragnathidae). *Animal Behaviour*, *63*(1), 175–182. https://doi.org/10.1006/anbe.2001.1878

Tsurui, K., Honma, A., & Nishida, T. (2010). Camouflage effects of various colour-marking morphs against different microhabitat backgrounds in a polymorphic pygmy grasshopper *Tetrix japonica*. *PLoS ONE*, *5*(7), e11446. https://doi.org/10.1371/journal.pone.0011446

Uva, V., Päckert, M., Cibois, A., Fumagalli, L., & Roulin, A. (2018). Comprehensive molecular phylogeny of barn owls and relatives (Family: Tytonidae), and their six major Pleistocene radiations. *Molecular Phylogenetics and Evolution*, *125*, 127–137. https://doi.org/10.1016/j.ympev.2018.03.013

Van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C. M., Solberg, E. J., & Saether, B.-E. (2013). Understanding scales of movement: animals ride waves and ripples of environmental change. *Journal of Animal Ecology*, *82*(4), 770–780. https://doi.org/10.1111/1365-2656.12045

Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack’s Principle. *The American Naturalist*, *100*(916), 687–690. https://doi.org/10.1086/282461

Wink, M., El-Sayed, A. A., Sauer-Gürth, H., & Gonzalez, J. (2009). Molecular phylogeny of owls (Strigiformes) inferred from DNA sequences of the mitochondrial cytochrome b and the nuclear RAG-1 gene. *Ardea*, *97*(4), 581–591. https://doi.org/10.5253/078.097.0425

Zimmerer, E. J., & Kallman, K. D. (1989). Genetic basis for alternative reproductive tactics in the pygmy swordtail, *Xiphophorus nigrensis*. *Evolution*, *43*(6), 1298–1307. https://doi.org/10.1111/j.1558-5646.1989.tb02576.x

Zingg, S., Ritschard, E., Arlettaz, R., & Humbert, J. Y. (2019). Increasing the proportion and quality of land under agri-environment schemes promotes birds and butterflies at the landscape scale. *Biological Conservation*, *231*, 39–48. https://doi.org/10.1016/j.biocon.2018.12.022