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Global biogeographical patterns in the diet of a cosmopolitan avian predator

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Abstract

Aim. The investigation of biogeographical patterns in the diet of widely distributed predators is essential to understand their ecology, life-history traits, and local adaptations. However, it is particularly challenging because of their wide distribution, broad trophic spectra and high ecological plasticity. Here, we described patterns of trophic ecology in a cosmopolitan nocturnal raptor, the common barn owl group, from a biogeographical perspective. We then compared variation in diet between barn owls living in the Americas (*T. furcata*), and those inhabiting in Europe, Middle-East and Africa (*T. alba*), thus hunting on different assemblages of prey types.

Location. World.

Taxon. Barn owl species complex.

Methods. We reviewed 790 studies reporting diet information of 971 locations (3,733,902 individual vertebrate prey), and investigated the variation in different diet parameters, reflecting taxonomic diversity, size of the prey and frequency of certain prey types according to geographic and climatic variables.

Results. While confirming that the barn owl is a selective mammal hunter with variable taxa constituting its staple food in different regions, we also found significant geographic and climatic trends in several diet parameters. Although prey composition differed among continents, most of the patterns, including an increase of proportion of mammal prey in cold environments, an increase in diet diversity with elevation, a decrease in small prey consumption from high to low latitudes and at increasing temperature, and a decrease in rodent predation in humid habitats, were similar between *T. furcata* and *T. alba*. A strong island effect was observed for all diet parameters.

Main conclusion. Our results indicate a generalized pattern of variation in barn owl diet across biogeographic regions, suggesting that similar prey communities occur in habitats with comparable ecological conditions and/or that different barn owl populations living in similar climate convergently evolved similar food preferences and hunting strategies.

Key words: biogeographical patterns, cosmopolitan species, diet diversity, diet generalism, diet specialism, predation, predator-prey interaction.

Short title: Global diet in the cosmopolitan barn owl

Introduction

An organism's diet is crucial in defining its ecological niche, and it plays a major role in determining individual fitness (Shoener, 1971). Investigating the spatial change in feeding habits is therefore fundamental to understanding how populations locally adapt and interact with the populations of the species to which they are ecologically linked (Sanford, Roth, Johns, Wares, & Somero, 2003). Indeed, ecological and climatic conditions directly affect presence and availability of organisms (Kaufman, 1995; Kaufman & Willing, 1998; Willig, Kaufman, & Stevens, 2003; Qian, Badgley, & Fox, 2009), thus producing a substantial impact on local diversity and composition in the diet of many species (Abrahams & Kattenfeld, 1997; Fedriani, Ferreras, & Delibes, 1998; Futuyma & Moreno 1988; Kaufman, 1995). This is especially the case for predators because variation in the distribution of potential prey species across latitudinal, altitudinal and climatic gradients has been shown to affect their predation strategies and food consumption (Clavero, Prenda, & Delibes, 2003; Lozano, Virgos, Cabezas-Díaz, & Mangas, 2006; Terraube & Arroyo, 2011; Zhou et al., 2011). In addition, it is well known that organisms vary in their phenotype according to environmental and climatic factors, and different phenotypes can be better adapted to exploit certain food resources than others (Arnold, 1977; Miller, Ament, & Schmitz, 2014; Roulin, 2004). The study of the intraspecific diet variation using a biogeographical approach on large geographical scale is therefore essential to understand predators' ecology and life-history traits. Unfortunately, with few relatively recent exceptions of continental-level analyses (Birrner, 2009; Clavero et al., 2003; Díaz-Ruiz et al., 2013; Goszczyński, Jedrzejewska, & Jedrzejewski, 2000; Lourenço, Santos, Rabaça, & Penteriani, 2011; Lozano et al., 2006; Terraube & Arroyo, 2011), trophic ecology of predators has been traditionally investigated at local or, at best, regional scales.

In addition, extensive ecological studies comparing variation in feeding habits among populations over a wide range of environmental conditions are also necessary to define whether a species is a diet specialist or generalist. Organisms are considered generalist when they rely on a large suite of food sources and can opportunistically modify their diet according to the abundance of each suitable food type. By contrast, trophic specialists mainly feed on a single food source irrespectively of its availability, and have a limited capacity to shift between different food types (Futuyma & Moreno, 1988; Glasser, 1982). However, the boundary between these two extremes is not well defined, and a continuum from generalization to specialization exists (Bernays, Singer, Rodrigues, 2004; Woo, Elliott, Davidson, Gaston, & Davoren, 2008). This is also the case at the within-species level, when populations of a given species use a large variety of resources, while other populations are instead

specialized on a single food source (Díaz-Ruiz et al., 2013; Goszczyński et al., 2000; Roth, Marshall, Murray, Nickerson, & Steury, 2007). Although spatiotemporal adjustments in diet composition are expected to be particularly crucial in determining survival and reproductive success, the mechanisms linking individual preference for a certain food have not yet been fully understood.

In the present study, we investigated variation in several diet parameters according to geographical and climatic factors in the cosmopolitan common barn owl group (*Tyto alba* species complex) across its entire global distribution range. To this purpose, we realized an extensive literature search and collated published information on the diet of this taxon collected at more than 950 locations across the globe. Sites for which diet data were available were located in all the continents (except for Antarctica where this taxon is not present) within the distribution ranges of the three phylogenetically distinct lineages of this species complex (Aliabadian, Alaei-Kakhki, Mirshamsi, Nijman, & Roulin, 2016; Uva, Päckert, Cibois, Fumagalli, & Roulin, 2018; Wink, El-Sayed, Sauer-Gürth, & Gonzalez, 2009). Although their taxonomic status has to be officially determined, under an eco-evolutionary perspective these evolutionary lineages can be considered as adaptive radiations occurring in geographically separated regions and producing a variety of local adaptations (see details in Romano, Séchaud, Hirzel, & Roulin, 2019; Uva et al., 2018): the Western barn owl (*T. alba*), living from South Africa to Southern Scandinavia, including Arabic Peninsula, Middle East, Madagascar, and all the African archipelagos in the Atlantic and Indian Oceans; the American barn owl (*T. furcata*), inhabiting from Patagonia to Southern Canada, including all the Caribbean, Hawaii and Galapagos islands; and the Eastern barn owl (*T. javanica*), occurring from Australia to Asia south of the Himalaya, including Tasmania and all the archipelagos in the Pacific Ocean. The investigation of this model system therefore provides the rare opportunity to compare variation in diet features among populations exposed to very different environmental and ecological conditions, as well as hunting on different assemblages of potential prey.

The barn owl diet has been widely studied through the analysis of pellets content, and small mammals invariably constitute its staple food source worldwide, with a variable presence of other prey types, such as birds, reptiles, amphibians, and invertebrates (summarized by Taylor, 2004). Given the large distribution range, its dietary composition and diversity vary among different regions, as shown by geographical studies at the country or continent level (see e.g. Flikweert, Prins, de Freitas, & Nijman, 2007; Herrera, 1974; Muñoz-Pedreros, Gil, Yáñez, Rau, & Möller, 2016; Obuch & Benda, 2009; Roulin, 2004; Schmidt, 1973; Trejo & Lambertucci, 2007) or comparative analyses of geographically distinct regions with similar climate (Jaksic, Seib, & Herrera, 1982). However, specific studies describing large-scale biogeographical patterns using a

quantitative approach are lacking (but see Taylor, 2004 for a general qualitative description of the diet in different continents), as well as the effects of latitude, altitude and climate on its dietary diversity and composition are unknown. In addition, whether barn owls capture their prey opportunistically in proportion to their availability or carefully select them remains a controversial issue. Many researchers have claimed that they hunt opportunistically (e.g. Avery, Avery, & Palmer, 2005; Bernard et al., 2010; Flikweert et al., 2007; Herrera, 1974; Love, Webon, Glue, Harris, & Harris, 2000; Taylor, 2004), but other studies have shown considerable differences between prey composition in the pellets and that recorded using trapping data in the field (e.g. Jaksić & Yáñez, 1979; Marti, 1974; Perrin, 1982; Yom-Tov & Wool, 1997; see also Heisler, Somers, & Paulin, 2016 for a multi-species study). In addition, experimental studies under controlled aviary conditions have also shown that barn owls select prey according to their size, activity and vulnerability (e.g. Dickman, Predavec, & Lyman, 1991; Embar, Mukherjee, & Kotler, 2014; Ille, 1991; Vanitha & Kanakasabai, 2009). A large-scale study may also help to define whether the consumption of some prey types, such as different categories of small mammals, varies spatially.

The main aim of the present study was to describe the biogeographical patterns in the trophic ecology of the barn owl across the globe and compare them among the different regions where it lives. Specifically, we analysed changes in consumption of main food groups (e.g. small mammals, rodents), diet diversity (Shannon index) and prey size in relation to geographical (latitude and elevation) and climatic variables (temperature and precipitation). Our ability to understand such biogeographical patterns also has important implications for the understanding of population dynamics and local adaptation, and also for developing efficient management programs for this avian predator, showing strong links to synanthropic habits.

Methods

Diet data

In order to collect reliable data on the barn owl diet across the globe, we collected published information on scientific papers, but also grey literature and Ph.D./master theses, adopting a procedure similar to that used in meta-analytic studies. We firstly collected all suitable studies (including associated supplementary information) on *ISI Web of Science*, *Scopus* and *Google Scholar* by combining the key words ‘barn owl’ or ‘*Tyto/T. alba/T. furcata/T. javanica*’ with ‘diet’,

‘predation’, ‘prey’ or ‘food’. Considering that the vast majority of studies on barn owl diet have been performed in Europe (see below), in order to enhance the representation of locations from other continents, a geographical term among ‘North America’, ‘South America’, ‘Middle East’, ‘Asia’, ‘Africa’, or ‘Australia’ was added to the search string. We also carefully screened the references in all the papers, as well as we asked authors for unpublished information, to obtain the broadest possible coverage of the literature. Publications in languages other than English (e.g. French, Spanish, German, Hungarian, Italian and Portuguese) were also included in our sampling.

We then selected the papers reporting at least 90 vertebrate food items (references can be requested from the authors) and where at least of 80% of mammalian prey were correctly identified at the genus level. However, when data were recorded on small islands we included locations with at least 50 identified prey. This was the case for four islands: Santiago (Rabaca & Mendes, 1997) and Fogo (Siverio, Tosco, & Castro, 2008) in Cape Verde, Isabela in the Galapagos (de Groot, 1983) and Porto Santo in Madeira (Siverio et al., 2008). We included information collected both in a single year and along many years, as well as in a single location and in geographical small regions (e.g. county, district or island). However, we excluded all the papers reporting information at a large geographical scale, like countries or large regions (e.g. Avery et al. 2005; Love et al. 2000), because the prey diversity is expected to increase according to the number of habitats included in the sampling. Finally, to limit the temporal variation in diet, we restricted our analyses to the information collected after 1940.

Information reported in different studies were entered separately in our dataset. However, we adopted specific data selection criteria in order to limit pseudoreplication of data. When the same study reported diet information on different locations, we pooled data of locations located in a radius of 80 km. When the same study reported diet information in different years and/or seasons data were also pooled. When different studies reported diet information in the same location, we used the one including the largest number of prey items identified. However, in a few cases, when the paper including the largest number of prey items provided only information on mammalian prey, for the analysis of proportion of mammal over the total vertebrate prey (see below) we used the information of the paper including the largest sample of vertebrate prey among those reporting this specific information. At the end of this procedure, our dataset included 790 different papers reporting diet information of 971 locations across the globe (717 *T. alba*, 214 *T. furcata*, 40 *T. javanica*; Table 1; Figure S1) for a total of 3,733,902 individual vertebrate prey items (3,319,553 *T. alba*, 371,974 *T. furcata*, 42,375 *T. javanica*; Table 1). Unfortunately, diet locations for *T. javanica* were relatively few, and, more remarkably, all the sites (with the exception of four datapoints in Malaysia, Indonesia and Vanuatu) were located at the extremes of its distribution range: in

Australia and India-Pakistan-Nepal (Figures 1a and S1). Such a biased distribution of datapoints prevented us from reliably analysing diet parameters according to the geographical and climatic variables using continuous covariates (see below). These data were therefore used for descriptive purposes, and the main analyses were performed on *T. alba* and *T. furcata* only.

For each location, we calculated the proportion of each terrestrial mammalian prey genus *i* (number of individuals of species *i* divided by the total number of terrestrial mammals consumed), and, when reported, the proportion of the terrestrial mammalian prey over the total amount of vertebrate prey (see Table 1 for sample size). Bats were not included in this count because they are a minor component of the barn owl diet (Roulin & Christe, 2013) and because many studies only focused on terrestrial mammals. Bats were therefore included among the other vertebrates, in addition to birds, amphibians, reptiles and, very rarely, fish. However, in the analyses of proportion of terrestrial mammals, we excluded the studies when the only other vertebrates collected were bats (i.e. we only included studies where classes of vertebrates other than mammals were included). We did not collect any information about invertebrate prey because only a small fraction of the papers reported reliable information about this food source, which, however, account for a very minimal part of the diet (see e.g. Muñoz-Pedreros et al., 2016; Obuch, Danko, & Noga, 2016; Obuch & Benda, 2009; Roulin, 2016; Schmidt, 1973; Trejo & Lambertucci, 2007). The proportion of each mammalian prey genus was then used to calculate the Shannon diversity index at the genus level. This was done because many studies did not report information at the species level and in order to account for variability in the species diversity among genus. In addition, the Shannon diversity index was calculated only on mammals 1) because they constitute the vast majority of barn owl prey across the globe; 2) because many papers were focused on mammals only; and 3) because usually other vertebrates were not properly identified at the genus level (e.g. in many cases they were generically reported as birds, reptiles or amphibians). Importantly, we used the Shannon index as a proxy of diet diversity rather than e.g. the number of genera predated in each location, also because this value does not depend on the number of prey items recorded (total: $t = 1.51$; $P = 0.13$; *T. alba*: $t = 1.34$; $P = 0.18$; *T. furcata*: $t = -0.68$; $P = 0.50$; *T. javanica*: $t = 0.78$; $P = 0.44$).

We also estimated the average body mass of each prey genus. However, for the rare cases when marked geographical difference in the weight of different species of the same genus occurred, we assigned different body mass to species inhabiting different regions (e.g. the genus *Suncus* in Europe is composed by some species weighing less than 10 g, but in Asia the only species predated by barn owls is the much larger *S. murinus*, which can weight more than 100 g). Finally, for a descriptive purpose, each prey genus was coded on the basis of its main exploited habitat: species living on the ground were defined as ‘terricolous species’, species living below the ground surface

were defined as ‘fossorial species’, while species living on trees or bushes were defined as ‘tree-dwelling species’.

Geographic and climatic variables

Locations where diet information was collected were converted into latitude and longitude coordinates. If the diet data were collected at regional scale, we assigned coordinates near the centre of the specified region. The same was done when diet information on nearby locations were pooled. For each pair of coordinates, we collected climatic information at a 30 arc-second spatial resolution, from the Worldclim dataset for the period 1970–2000 (www.worldclim.org; Fick, & Hijmans, 2017), which is a good proxy for the climatic variables recorded in the entire timespan where diet data were collected (see Romano et al., 2019). Since the barn owl is a resident species, values of the mean annual temperature and total annual rainfall were associated with each diet data. The elevation of each location was also recorded. However, considering that many diet data were obtained after pooling data of different sites and that many others were collected by the authors at a regional scale (see above), we extracted information on mean annual temperature, mean annual rainfall and mean elevation over a radius of 20 km from the point where the geographical coordinates were set. This approach, which was used in our recently published papers (see also Romano et al., 2019; Romano, Séchaud, & Roulin, 2020), therefore allowed us to account for the possible heterogeneity in elevation and climatic conditions of different, although nearby, sites where diet data were collected. In addition, it also allowed us to account for the variation in climatic/elevational conditions experienced by barn owls when hunting the prey in different neighbouring habitats. Finally, we note that we previously showed that climatic data extracted in a single geographic point, over a 20-km radius or over a 50-km radius from any given pair of coordinates are strongly correlated (temperature: $r > 0.97$; rainfall: $r > 0.96$; Romano et al., 2019).

Statistical analyses

To examine variation in diet parameters according to geographical and climatic factors we used generalized linear models using the *glmmTMB* package (Brooks et al., 2017) in R (version 3.5.1). Variation in diet variable (see below) was analysed separately for *T. alba* and *T. furcata* in two sets of analyses (see also Romano et al. 2019). In the *geographic models* we included as predictors hemisphere, a dichotomic factor indicating if the diet datum was collected on an island (coded as 1) or a mainland (coded as 0), absolute latitude and elevation, as well as the absolute latitude by

hemisphere interaction. In the *climatic models*, we included mean annual temperature, the total annual rainfall and their interaction as predictors. We distinguished between two sets of models because climatic and geographical factors, although intrinsically associated (e.g. latitude is strongly associated with temperature variation) may represent alternative/complementary explanations to account for diet variation. To obtain scale-independent estimates of the covariation between diet and predictors and to compare results of different lineages, all continuous covariates were standardized within each taxon. To account for non-random distribution of locations, and therefore for the presence of different prey types across geographical gradients, in all the models we accounted for spatial autocorrelation, by adding an exponential correlation structure considering the distances between all the pairs of latitude-longitude coordinates. We finally added the factor ‘continent’ as a random effect in order to statistically control for difference in prey communities among large biogeographic regions.

As dependent variables, we used different diet features in terms of diversity, taxonomy and size of the prey, which were modelled depending on their error distribution. Diet diversity (Shannon index) was analysed using a normal distribution, while proportion of mammals, proportion of small prey (smaller than 50 g), proportion of mammals that are rodents, and proportion of genus *Mus* using a binomial distribution with the success/failure formula, thus statistically accounting for the sample size of each location. We analysed variation in the proportion of small prey rather than on mean prey size because all the species of each genus preyed are heavier or lighter than 50 g. We decided to limit the analyses to these categories of prey because they are the most abundant in the barn owl diet (e.g. most of the prey are small rodents; the genus *Mus* is the only widespread everywhere; see Table 1), thus allowing the comparison between different regions of the world.

Results

Global diet composition

Table 1 and Figure 1 show a raw summary of the main prey types collected in barn owls’ pellets in different regions of the globe. The barn owl diet is invariably composed mainly by terrestrial mammals, that account for 75-95% of individual captured prey depending on the continent. The only exceptions are the Caribbean islands and Madagascar, where these prey types account for less than 60% of the total captured, while the remaining is mainly composed by small birds and reptiles. On the mainland, the smallest proportion of mammals is recorded in the xeric Northern Africa,

where this prey type account for ca. 75% of the food consumed. The largest diversity of genera preyed is observed in South America (70 genera) and Sub-Saharan Africa (54), followed by North America (44) and Europe (34). On the other hand, on the islands, with the exception of the British Isles (16), the number of genera found in the pellets is always smaller than 10, reaching the minimum value on the Caribbean islands where barn owls hunt only three species of introduced mammals (i.e. mice, rats and rabbits). On the mainland, the proportion of genera smaller than 50 g is always comprised between 0.50 and 0.61, with the only exceptions of Asia (0.33) and Australia (0.79). Although the prey smaller than 50 g constitute just over 50% of the prey potentially available across the globe, our analyses confirm that this prey type is the bulk of the diet, representing more than 70% of the prey everywhere in the world, with the exception of Asia, Central America, Caribbean islands and Madagascar, where prey are generally larger, and the *Rattus spp.* are particularly abundant in the pellets.

Most of the prey are terricolous rodents, which constitute the staple food source in all the continents. However, in Asia and Europe where insectivores are also an essential component of the diet representing more than 25% of the prey, percentage of rodents is smaller than for the other continents. Among rodents, the two main consumed families are murids (Muridae) and cricetids (Cricetidae). The former is particularly abundant in the diet of African, Asian, Australian and Caribbean barn owl, the latter in North and South America, while in Europe and Middle East both of them exceed the 20% of the prey. In the Americas, heteromyid (Heteromyidae) rodents are also a non-negligible part of the diet, especially in Central America where they represent around 24% of the prey. Marsupials are also an important component of the Australian barn owl diet (ca. 6%), and they can be found at smaller percentages in the pellets of American populations. Small lagomorphs and carnivores (e.g. mustelids) are occasionally hunted in different continents. Finally, small primates (genus *Microcebus*) constitutes almost the 6% of the diet in Madagascar, and nesomyid (Nesomyidae) rodents around 5% of the diet of the African barn owls living south of the Sahara desert.

Geographical variation in diet composition

Percentage of mammals. In both *T. alba* and *T. furcata*, the proportion of terrestrial mammals in the diet increases with latitude (Table 2). In addition, in both lineages the proportion of vertebrate prey that are not terrestrial mammals is larger on islands than on mainland, and in the Western barn owl it also increases with elevation (Table 2).

Shannon Diversity Index. In both lineages, diet diversity increases with elevation and is smaller on islands than on mainland (Table 2). In addition, in the Western barn owl it also increases with latitude and is larger in the Southern than in the Northern hemisphere.

Proportion of prey smaller than 50g. Small prey proportion increases with latitude both in the Americas and in the Afro-Palearctic region, with a steeper relationship in the Northern hemisphere (Table 2). In addition, in *T. alba* it is smaller on islands than on mainland. Moreover, in the two lineages there is an opposite effect of the hemisphere: in *T. furcata* prey are smaller in the Southern hemisphere, while in the case of *T. alba* it is smaller in the Northern hemisphere.

Proportion of rodents. In *T. alba*, proportion of rodents decreases with latitude, and especially in the Northern hemisphere, where this component of diet is also smaller than in the Southern one (Table 2). No significant macro-ecological patterns are observed in *T. furcata*.

Proportion of genus Mus. Proportion of mice in the diet is larger close to the Equator rather than at high latitudes as well as on islands than on continents, both in the American and Western barn owl, but in the former this is especially the case for the Northern hemisphere (Table 2). In addition, it significantly decreases with elevation in *T. furcata*, while in *T. alba* it is larger in the Northern than in the Southern hemisphere.

Variation in diet composition according to climate

Percentage of mammals. The proportion of mammals in the diet decreases with temperature in both *T. alba* and *T. furcata*. In addition, in the Western barn owl it increases with rainfall (Table 3).

Shannon Diversity Index. In *T. alba* it increases at lower temperatures, while no variation according to climate was observed in the Americas (Table 3).

Proportion of prey smaller than 50g. Small prey proportion decreases with temperature both in the Americas and in the Afro-Palearctic region. It also decreases at increasing level of precipitation in *T. alba*, and in *T. furcata* this is the case only in cold climates (Table 3).

Proportion of rodents. Proportion of rodents in the diet decreases with rainfall both in the Western and in the American barn owl (Table 3). In addition, it also increases with temperature in *T. alba*, where it also emerged an interaction between these climatic factors: rodents are less abundant in environments characterized by high temperature and high precipitation.

Proportion of genus Mus. Proportion of *Mus* in the diet decreases with rainfall in *T. alba*, while it increases with temperature in *T. furcata*, especially at decreasing level of precipitation (Table 3).

Discussion

In this study we investigated, for the first time in any animal taxon, the spatial variation in diet composition of a cosmopolitan predator at the worldwide scale (but see Birrer, 2009 for a descriptive study of the global diet of another raptor, the long-eared owl *Asio otus*). We found that all the analysed parameters of the barn owl diet show a significant association with climatic and/or geographic factors. Although a large variation in prey composition was observed among different areas of the globe, we could find many patterns which are similar between barn owls living in the Americas and the ones inhabiting in the Afro-Palearctic region. Interestingly, variation in each diet parameter was significantly predicted by at least one climatic/geographic variable in the same direction in the two lineages (Figure 2). More remarkably, most of the relationships between diet parameters and, respectively, absolute latitude, elevation, temperature, rainfall and island vs. mainland are in the same direction between the Western and the American barn owls. This is the case for all the significant relationships (Tables 2 and 3; Figure 2), with the exception of the effects of latitude on the proportion of rodents, and the effect of the temperature by rainfall interaction in predicting the proportion of rodents and mice. These observations thus indicate a very generalized pattern of variation in barn owl diet across the globe, with differences emerging only when the investigation is conducted at a low taxonomic level (i.e. rodents and *Mus spp.*), while the general diet features (e.g. proportion of mammals, proportion of small prey) show similar trends in different biogeographic regions.

Given the correlative nature of the study, we can only speculate why such common patterns occur. On the one hand, they might simply reflect the relative abundance of prey types available at each location, with assemblages of potential prey frequency being similar among environments characterized by comparable ecological conditions. However, the observation that similar geographic/climatic clines were found also when a considerable difference in geographic variation in a given prey type occurs between *T. alba* and *T. furcata* (e.g. in *T. alba* prey are larger in the southern hemisphere, while in *T. furcata* is the opposite; Figure 1d, Table 2) or when the relative abundance of a prey type is very different between the distribution ranges of the two lineages (e.g. proportion of *Mus* which is considerably larger in *T. alba* than in *T. furcata*; Figure 1f) testifies against this possibility, at least for some diet parameters. On the other hand, it is also possible that different barn owl populations living in geographically distinct regions with comparable climate were convergently selected to have similar food preferences, exploit similar resources, or evolve

similar hunting strategies. Below we discuss the main results while trying to interpret whether each observed specific pattern can be mainly explained by either of the two aforementioned possibilities, geography and climate. Conversely, although we are aware that variation in diet composition could be also affected by competition with other predators (e.g. Jaksić et al., 1982), potentially relying on the same resources (e.g. other raptors eating prey of a given size, thus constraining the barn owl to select prey of the remaining sizes), we cannot evaluate this because we do not have a full picture of the distribution and the local diet of all possible competitors across the entire barn owl distribution range. Our results should thus be considered with this caveat in mind.

Among the patterns consistently observed in the two lineages, we found that barn owls living in cold climates (i.e. higher latitudes and lower temperatures) generally consume a relatively larger proportion of mammals than in warm environments, despite, with a few exceptions (see Figure 1b and Table 1), mammalian prey invariably constitutes more than 70-80% of the prey. This pattern was not expected because animals, including the mammalian prey of the barn owl, are more diverse and abundant closer to the equator (Hillebrand, 2004; Kaufman, 1995; Kaufman & Willing, 1998; Qian et al., 2009). A selective hunter of small mammals should have thus been facilitated in consuming such a prey type at lower latitudes. It is thus likely that populations adapted to colder climates evolved to be more specialized in mammal hunting than those living in warm (and dry, but only in *T. alba*) habitats. It is therefore not surprising that the climatic model better explains variation in this diet parameter in *T. alba*, while in *T. furcata* the observed pattern seems to be more associated with geographical distribution of this prey type. However, because other potential prey, as lizards, birds and bats, show a similar latitudinal gradient in diversity (e.g. Hillebrand, 2004; Rhabek & Graves, 1999; Stevens & Willig, 2002), it is also possible that even a moderate generalist predator could easily shift between different prey types if they are particularly abundant (Roulin & Dubey, 2012; Roulin & Christe, 2013; Roulin, 2016). This pattern is particularly strong in the northern hemisphere, consistently with a previous study on a diurnal generalist raptor, the Montagu's harrier (*Circus pygargus*; Terraube & Arroyo, 2011), possibly because in Europe and North America the hunting grounds are mainly represented by cultivated fields, thus making easier the capture of small mammals living therein than in natural environments, where prey have more chances to escape and hide. The possibility that the barn owl changed its diet composition according to the human-induced environmental changes is corroborated by the evidence that pre-agricultural zooarchaeological assemblages of prey from Europe and North America are different from the current ones collected in the same locations (e.g. Lyman, 2012; Lyman & Lyman, 2003; Vigne, 1992).

Concerning the diversity of mammal in the diet, we showed a positive altitudinal trend, with populations living at high elevation relying on a larger prey diversity than those living at the sea level (see Figure 1b showing that many peaks of diversity are associated with mountain ranges, like Andes and Rocky Mountains in *T. furcata*, and Alps, Pyrenees as well as Central and Southern African highlands in *T. alba*). This finding is not surprising because it has been previously documented in several regions across the globe that small mammal assemblages generally show a peak of diversity at medium and high elevations (Bateman, Kutt, Vanderduys, & Kemp, 2010; Lomolino, 2001; McCain, 2005; Ruggiero & Kitzberger, 2004). As the barn owl is not common in high mountain habitats (e.g. mountain tundra), such an increase in diet diversity would probably simply reflect the larger diversity in potential prey according to elevation, as suggested by the observation that in both lineages the geographic models are better supported than the climatic models. In addition, in the Western barn owl diet diversity is also predicted positively by latitude and negatively by temperature. This finding contrasts with a previous comparative study showing a decrease with latitude in the diet diversity of the barn owl both in Europe and in North America (Korpimäki & Marti, 1995). However, the two findings are not directly comparable because the study by Korpimäki & Marti (1995) relied on a much smaller sample of locations (i.e. 23 in Europe and 40 in North America) and they did not account for spatial autocorrelation of their data. In addition, their diversity indexes were calculated including all the prey captured by the barn owls (see also Taylor, 2004), while we focused on the mammal diversity only. Finally, and importantly, they focused on the continents located in the boreal hemisphere only, while our analyses included locations across the entire barn owl distribution, thus possibly indicating that in Europe and North America diet diversity is negatively correlated with temperature and latitude, while from a global perspective the opposite is the case (Figure 1c).

Another interesting result is that the proportion of small prey in the diet considerably increases in colder environments. This is the case in both lineages despite the overall difference in mean prey size between the Americas and the Afro-Palearctic region, and even if in *T. alba* geography alone better explains this finding while the opposite holds true for *T. furcata*. However, regardless of the fact that this pattern is mainly driven by geography or climate, such an observation is in contrast with the ecogeographic Bergmann's rule, postulating that animal body size should decrease with increasing temperature for thermoregulatory reasons (Bergmann, 1847). Mammal body size, including that of species hunted by barn owls, generally follows such a rule in all the continents included in our analyses (Ashton, Tracy, & Queiroz, 2000; Blackburn & Hawkins, 2004; Rodríguez, López-Sañudo, & Hawkins, 2006; but see Ochocińska & Taylor, 2003). This suggests that the observed trend in prey size was not linked to a higher abundance of smaller mammals at

higher latitudes and lower temperatures, as also suggested by the observation that the proportion of small genera among those available overall is rather constant across the distribution ranges of both the lineages. We note that such a pattern could be due to the presence of insectivores (e.g. Soricidae and Afrosoricidae; see also Cotgreave & Stockley, 1994), which represent a non-negligible fraction of the diet at temperate and boreal regions, and which are generally smaller than rodents. However, the same trends in the proportion of small prey were observed when the analyses were limited to rodents only (details not shown for brevity). These combined observations thus indicate that barn owls living in relatively cold environments might be specialized in hunting small prey, irrespectively of their abundance. This result is consistent with our recent findings that bill size decreases in cold environments in all the barn owl lineages (Romano et al., 2020), according to the prediction of Allen's rule (Allen, 1877) and the role of the ramphotheca as a functional heat-exchange surface used by birds to maintain and disperse body heat (e.g. Tattersall, Arnaout, & Symonds, 2017). It is thus possible that a decrease in bill size due to thermoregulatory functions resulted in specialization in consuming smaller mammals. However, we note that we did not collect data on ingested biomass, and therefore we cannot properly quantify the proportion of biomass that small prey items compose worldwide. For example, we cannot exclude that even when small prey constitutes a very large proportion of the food items they can still represent a small fraction of the biomass ingested.

Conversely, the smaller proportion of rodents in relatively humid environments might suggest that in these areas barn owls can exploit other food sources which are more abundant in such climatic conditions. This is the case for small marsupials and other mammals living in the rainy forested areas of Central-South America and Africa respectively, as well as insectivores in northern humid regions of Europe and North America. A similar consideration can be done for the presence of *Mus spp.* in the diet, which should reflect the abundance and distribution of this genus, being more common at lower latitudes and elevations, as well as in warm environments.

It is noteworthy that all the analyses show a strong island effect, with insular populations relying on a smaller proportion of mammals, mainly represented by synanthropic species, like mice and rats, thus resulting in a smaller prey diversity, than those living on the mainland. The smaller mammal proportion in the diet of insular populations, and the consequent lower diet diversity, can be easily explained by the observation that small islands usually host a minimal number of rodent species, thus constraining the owls to shift their diet to the other vertebrate food sources, like reptiles, birds and amphibians (see also Roulin & Dubey, 2012), consistently with the theory of feeding specialization (Futuyma & Moreno, 1988). In addition, the prey captured by insular owls are generally larger than on mainland, probably because of the large presence of rats.

In conclusion, biogeographical variation in the feeding habits of American and Afro-European barn owls are associated with geographical and climatic variables, which affect the availability of different potential food sources and/or promote the evolution of local diet specialization. On the whole, our study confirms that this nocturnal raptor is a specialist in small mammals hunting across its entire range of distribution, suggesting that it generally does not behave as opportunistic, nonselective vertebrate predator. Indeed, the proportion of small mammals in the diet is invariably larger than the proportion of small genera potentially available to the barn owls across the globe. However, when the availability of small mammal is scarce, like the islands and xeric regions, this species is able to target other prey types. This is in line with the theory of feeding specialization, predicting an increase of consumption of other food sources when the preferred one becomes less abundant (Futuyma & Moreno, 1988). However, it is also highly generalist in small mammal consumption with different taxa that constitute the bulk of the diet in different part of the world, consistently with its recorded capacity to switch from one main prey to another prey type which in the past have been of secondary importance (Bernard et al., 2010; Tores, Motro, Motro, & Yom-Tov, 2005). This is particularly clear in Australia, where the main prey are allochthonous murids, and specifically mice and rats, rather than endemic marsupials, which constitute only a small fraction of the diet. Such a large flexibility in hunting behaviour and high adaptability to environmental changes are probably key aspects for its ecological success. Understanding the patterns in the trophic ecology of the barn owl group, the most widespread owl taxon in the globe, will enhance our knowledge of the geographical variation in its abundance and behaviour, and can be therefore useful to improve the management and conservation of local populations of this cosmopolitan raptor.

Data availability. The dataset used for manuscript is reported in Table S1.

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Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. *Journal of Biogeography*, 38, 137-147.

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 different morphological and chromatic traits and in their covariation by combining disciplines of evolutionary ecology, biogeography, behavioural ecology, genetics, and population genetics/genomics. Specific aims of our research are to determine the adaptive function of alternative phenotypes, identify how ecological, social and physiological factors influence and maintain inter-individual variation in melanin-based coloration and the other associated phenotypic traits, as well as disclose the mechanisms favouring the highly adaptability of different environmental conditions of this cosmopolitan raptor.

Table legends

Table 1. Summary of the diet diversity, mean prey size and proportion of the main prey types collected in barn owls' pellets in different regions of the globe. Prey categories included in the table represent prey types found in the diet of barn owls living in at least two continents, irrespectively of their relative abundance. Values included in the table are the arithmetic means between values recorded at each location included in our sample.

Table 2. Variation in proportion of mammals, Shannon Diversity Index, proportion of prey smaller than 50 g, proportion of rodents, and proportion of genus *Mus* in the diet of the Western (*T. alba*) and the American (*T. furcata*) barn owls according to absolute latitude, elevation, hemisphere (positive values indicate that the dependent variable is higher in the southern hemisphere), island vs. mainland, and hemisphere by latitude interaction. Coefficients of main terms refer to models excluding the interaction between hemisphere and absolute latitude. Bold type indicates statistical significance.

Table 3. Variation in proportion of mammals, Shannon Diversity Index, proportion of prey smaller than 50 g, proportion of rodents, and proportion of genus *Mus* in the diet of the Western (*T. alba*) and the American (*T. furcata*) barn owl according to mean annual temperature, annual rainfall and their interaction. Coefficients of main terms refer to models excluding the interaction between mean annual temperature and annual rainfall. Bold type indicates statistical significance.

Table 1.

	Europe	British Isles	Middle East	Northern Africa	Sub-Saharan Africa	Cape Verde and Canaries	Madagascar	North America	Central America	Caribbean	Galapagos	South America	Asia	Australia ³
Locations	542	43	33	31	50	6	7	104	15	8	2	84	15	24
Total Vertebrate Prey	2'782'595	377'704	32'312	44'688	44'595	18'040	6'344	263'809	5'446	11'218	2'317	88'514	25'245	15'874
Number of Genus	34	16	26	19	54	4	7	44	23	3	5	70	10	14
Number of Genus Smaller than 50 g	17	9	13	11	33	2	5	25	16	1	2	38	3	11
Proportion of Mammals¹	0.946	0.969	0.855	0.753	0.900	0.754	0.595	0.959	0.895 ²	0.552	0.746	0.906	0.903	0.894
Shannon Diversity Index	1.928	1.689	1.647	1.279	2.005	0.508	1.160	1.631	1.611	0.573	0.787	1.886	1.605	1.091
Mean Prey Size (g)	25.75	27.55	40.56	30.78	46.50	27.19	55.05	53.15	62.44	79.30	42.52	48.67	72.84	33.97
Proportion of Prey Smaller than 50g	0.970	0.942	0.746	0.869	0.725	0.922	0.644	0.758	0.631	0.334	0.721	0.800	0.577	0.889
Proportion of Terricolous Prey	0.988	0.994	0.992	0.995	0.956	1	0.939	0.945	0.974	1	0.999	0.953	0.998	1
Proportion of Rodents	0.731	0.753	0.875	0.894	0.848	0.990	0.840	0.910	0.972	0.999	1	0.966	0.580	0.937
Proportion of Insectivores	0.268	0.247	0.125	0.104	0.149	0.005	0.101	0.085	0.023	0	0	0.003	0.420	0
Proportion of Marsupials	0	0	0	0	0	0	0	0.0001	0.004	0	0	0.024	0	0.063
Proportion of Carnivores	0.0001	<0.0001	0	<0.0001	<0.0001	0	0	<0.0001	0	0	0	0	0	0
Proportion of Lagomorphs	0.0002	<0.0001	<0.0001	0.001	0	0.005	0	0.005	<0.0001	0.0001	0	0.003	0	0.0003
Proportion of Murids	0.287	0.328	0.663	0.872	0.777	0.990	0.838	0.046	0.146	0.999	0.999	0.080	0.577	0.937
Proportion of Cricetids	0.442	0.425	0.200	0	0	0	0	0.724	0.533	0	0	0.842	0	0
Proportion of Heteromyids	0	0	0	0	0	0	0	0.082	0.238	0	0	0.005	0	0
Proportion of <i>Mus spp.</i>	0.113	0.039	0.346	0.582	0.061	0.917	0.397	0.028	0.055	0.259	0.721	0.056	0.212	0.506
Proportion of <i>Rattus spp.</i>	0.016	0.049	0.052	0.045	0.016	0.073	0.440	0.010	0.147	0.741	0.278	0.024	0.240	0.111

Notes:

1: Number of locations where Proportion of Mammals was collected: Europe = 371, British Isles = 40, Middle East = 31, North Africa = 30, Sub-Saharan Africa = 38, Cape Verde and Canaries = 6, Madagascar = 7, North America = 81, Central America = 10, Caribbean = 8, Galapagos = 2, South America = 68, Asia = 14, Australia = 20

2. This value does not consider a location of a small island where only 5 out of 208 were mammals (Velarde et al., 2007). Including this datum, the average proportion of mammals is 0.816.

3. A study from Vanuatu (Ineich et al., 2012) was excluded from the calculation. All the prey were *Rattus spp.*.

Table 2.

Predictor	<i>Tyto alba</i>			<i>Tyto furcata</i>		
	Coefficient (SE)	t	P	Coefficient (SE)	t	P
<i>Proportion of mammals</i>						
AIC	5665.203			1621.679		
Intercept	3.101 (0.283)			3.538 (0.158)		
Absolute latitude	0.599 (0.126)		4.74 < 0.001	0.515 (0.126)		4.08 < 0.001
Hemisphere	0.450 (0.346)		1.30 0.19	-0.224 (0.244)		-0.92 0.36
Elevation	0.299 (0.080)		3.74 < 0.001	0.116 (0.116)		1.00 0.32
Island	-0.551 (0.189)		-2.92 0.003	-2.107 (0.465)		-4.53 < 0.001
Absolute latitude × Hemisphere			-1.43 0.15			-1.72 0.08
<i>Shannon Diversity Index</i>						
AIC	769.3565			351.9597		
Intercept	1.728 (0.136)			1.556 (0.134)		
Absolute latitude	0.109 (0.051)		2.15 0.032	0.008 (0.078)		0.11 0.91
Hemisphere	0.686 (0.135)		5.09 < 0.001	0.193 (0.198)		0.97 0.33
Elevation	0.092 (0.024)		3.82 < 0.001	0.113 (0.052)		2.15 0.032
Island	-0.364 (0.080)		-4.58 < 0.001	-0.702 (0.217)		-3.24 0.001
Absolute latitude × Hemisphere			0.15 0.88			1.25 0.21
<i>Proportion of small prey</i>						
AIC	6816.765			2336.627		
Intercept	3.576 (0.433)			1.464 (0.345)		
Absolute latitude	0.582 (0.120)		4.86 < 0.001	0.941 (0.221)		4.26 < 0.001
Hemisphere	-1.499 (0.357)		-4.20 < 0.001	1.343 (0.543)		2.47 0.014
Elevation	0.108 (0.079)		1.36 0.17	0.324 (0.176)		1.84 0.07
Island	-1.117 (0.209)		-5.35 < 0.001	-0.776 (0.711)		-1.09 0.28
Absolute latitude × Hemisphere			-2.97 0.003			-4.18 < 0.001
<i>Proportion of rodents</i>						
AIC	9245.736			1693.857		
Intercept	1.929 (0.349)			5.715 (1.163)		
Absolute latitude	-0.227 (0.091)		-2.49 0.013	0.446 (0.269)		1.66 0.10
Hemisphere	-0.994 (0.269)		-3.70 < 0.001	-0.306 (1.142)		-0.27 0.79
Elevation	-0.036 (0.057)		-0.63 0.53	-0.245 (0.194)		-1.26 0.21
Island	0.208 (0.153)		1.36 0.17	1.894 (1.050)		1.81 0.07
Absolute latitude × Hemisphere			2.84 0.005			0.83 0.41
<i>Proportion of Mus</i>						
AIC	7990.904			1380.378		
Intercept	-2.851 (0.266)			-5.867 (0.407)		
Absolute latitude	-0.490 (0.199)		-2.47 0.014	-0.728 (0.296)		-2.45 0.014
Hemisphere	-1.797 (0.681)		-2.64 0.008	-0.662 (0.625)		-1.06 0.29
Elevation	-0.105 (0.131)		-0.80 0.42	-0.819 (0.295)		-2.77 0.006
Island	1.046 (0.426)		2.46 0.014	2.378 (1.053)		2.26 0.024
Absolute latitude × Hemisphere			0.69 0.49			-2.09 0.037

Table 3.

Predictor	<i>Tyto alba</i>			<i>Tyto furcata</i>		
	Coefficient (SE)	t	P	Coefficient (SE)	t	P
<i>Proportion of mammals</i>						
AIC	5639.009			1635.541		
Intercept	3.388 (0.069)			2.864 (0.441)		
Temperature	-0.716 (0.070)	-10.20	<0.001	-0.522 (0.145)	-3.61	<0.001
Rainfall	0.246 (0.069)	3.56	<0.001	-0.006 (0.122)	-0.05	0.96
Temperature × Rainfall		-1.71	0.09		-1.42	0.15
<i>Shannon Diversity Index</i>						
AIC	791.3606			361.4838		
Intercept	1.881 (0.130)			1.459 (0.194)		
Temperature	-0.177 (0.051)	-3.45	<0.001	-0.059 (0.082)	-0.72	0.47
Rainfall	0.027 (0.028)	0.96	0.34	-0.034 (0.063)	-0.54	0.59
Temperature × Rainfall		-0.89	0.38		0.86	0.39
<i>Proportion of small prey</i>						
AIC	6838.903			2331.687		
Intercept	3.310 (0.381)			1.697 (0.436)		
Temperature	-0.768 (0.121)	-6.35	<0.001	-1.107 (0.232)	-4.77	<0.001
Rainfall	-0.243 (0.075)	-3.26	0.001	-0.017 (0.194)	-0.09	0.93
Temperature × Rainfall		-0.25	0.80		-1.99	0.047
<i>Proportion of rodents</i>						
AIC	9217.205			1693.812		
Intercept	1.547 (0.175)			5.808 (1.158)		
Temperature	0.316 (0.091)	3.48	<0.001	0.123 (0.243)	0.51	0.61
Rainfall	-0.252 (0.051)	-4.89	<0.001	-0.437 (0.200)	-2.19	0.029
Temperature × Rainfall		-2.28	0.022		1.22	0.22
<i>Proportion of Mus</i>						
AIC	7790.277			1390.877		
Intercept	-2.870 (0.223)			-5.963 (0.364)		
Temperature	0.262 (0.161)	1.62	0.10	1.091 (0.322)	3.39	0.001
Rainfall	-0.361 (0.130)	-2.77	0.006	-0.159 (0.313)	-0.51	0.61
Temperature × Rainfall		1.21	0.23		-2.50	0.013

Figure legends

Figure 1. Geographic variation in different diet parameters of the barn owl species complex: a) recovery sites of all the specimens included in the analyses; b) proportion of mammals; c) Shannon Diversity Index; d) proportion of prey smaller than 50 g; e) proportion of mammals that are rodents; f) proportion of genus *Mus*. For the maps between b) and f), an Inverse Distance Weighted (IDW) with a power value of 1 was used. For each cell size of 1°, the 20 closest data points were taken into account and a buffer of 500 km around each point was also included.

Figure 2. Summary of the main effect of absolute latitude, elevation, mean annual temperature and total annual rainfall on a) proportion of mammals; b) Shannon Diversity Index; c) proportion of prey smaller than 50 g; d) proportion of rodents; e) proportion of genus *Mus* in the diet of *T. alba* (red dots) and *T. furcata* (blue dots). Full dots represent statistically significant relationships. Mean values are the estimates of the models reported in Tables 2 and 3, and refer to standardized values within lineages. Error bars represent standard errors.