



Similar patterns of local barn owl adaptation in the Middle East and Europe with respect to melanic coloration

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The maintenance of phenotypic variation is a central question in evolutionary biology. A commonly suggested mechanism is that of local adaptation, whereby different phenotypes are adapted to alternative environmental conditions. A recent study in the European barn owl (*Tyto alba*) has shown that natural selection maintains a strong clinal variation in reddish pheomelanin-based coloration. Studies in the region where phenotypic variation in this owl is the highest in Europe have further demonstrated that dark-reddish and pale-reddish owls exploit open and wooded habitats, predate voles and wood mice, and are long-tailed and short-tailed, respectively. However, it remains unclear as to whether these traits evolved as a consequence of allopatric evolution of dark colour in northern Europe and white colour in southern Europe, during which owls could have also evolved different morphologies and foraging behaviour. This scenario implies that covariation between coloration and foraging behaviour could be a specificity of the European continent, which is not found in other worldwide-distributed populations. To investigate this issue, we studied a barn owl population in the Middle East. The results obtained show that, as in Central Europe, dark-reddish female owls breed more often in the open landscape than their pale-reddish female conspecifics, their offspring are fed with more voles than Muridae, and they are longer-winged and longer-tailed. These findings indicate that, in the barn owl, the association in females between pheomelanin-based coloration and foraging behaviour and morphology is not restricted to the European continent but may well evolve in sympatry in many barn owl populations worldwide. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **106**, 447–454.

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INTRODUCTION

Spatially-heterogeneous environments can select for different phenotypes that are adapted to specific local environmental conditions. For example, in many animals differently coloured individuals exploit alternative habitats (Roulin, 2004a) because colour morphs confer differential camouflage (Hoekstra, Krenz & Nachman, 2005) or because they are associated with alternative physiological properties that

provide maximal fitness benefits in different habitats (Sirkiä, Virolainen & Laaksonen, 2010). Studying local adaptation is therefore of importance for understanding how phenotypic diversity and its underlying genetic basis persist within and between populations (Kawecki & Ebert, 2004), as well as for explaining why different genotypes breed in alternative habitats to which they are best adapted (matching habitat choice; Edelaar, Siepielski & Clobert, 2008).

Numerous examples of locally-adapted phenotypes have been reported in the literature (Galloway & Fenster, 2000; Laine & Tellier, 2008), and a commonly advocated scenario to explain their initial emergence is that of allopatric evolution (Taberlet *et al.*, 1998).

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Physical barriers such as a river or mountain can divide a species into separate populations where selection favours specific phenotypic characteristics adapted to the prevailing environmental conditions. Once gene flow between these populations is restored in a so-called zone of secondary contact, interbreeding between two morphs can occur, provided that the level of genetic differentiation between individuals originating from different allopatric populations is not sufficiently pronounced to prevent fertile hybrids. If one morph does not outcompete the other, a genetic polymorphism is established. A potential mechanism that would allow morphs to coexist in the long-term in the zone of secondary contact is that of local adaptation, whereby each morph is adapted to a particular habitat and preferentially breeds there (Ravigné, Olivieri & Dieckmann, 2004; Edelaar *et al.*, 2008). Allopatric evolution is suggested to explain the emergence of genetic colour polymorphism (Roulin, 2004a), such as in the lesser snow goose (*Chen caerulescens caerulescens*) (Cooke, Parkin & Rockwell, 1988).

The European barn owl (*Tyto alba alba* and *Tyto alba guttata*) offers a suitable model by which to illustrate the potential role of allopatric evolution in the establishment of a genetic colour polymorphism and its evolutionary implications. On the European continent, barn owls vary continuously, from dark-reddish pheomelanic in northern Europe to white in southern Europe (Roulin, 2003), suggesting an allopatric evolution of these two colour morphs. This plumage trait is strongly heritable ($h^2 = 0.81$; Roulin & Dijkstra, 2003), and the strong clinal variation is maintained by selection, as recently shown in a study comparing the magnitude of differentiation between European populations in coloration (P_{ST}) with that of neutral genetic markers (F_{ST}) (Antoniazza *et al.*, 2010). Differentiation in coloration was so pronounced (in striking contrast to differentiation at neutral genetic markers, which was very weak on the scale of the European continent) that our estimates are unlikely to be biased (Edelaar, Burraco & Gomez-Mestre, 2011). This implies that selection to be dark-reddish in northern Europe and whitish in southern Europe is sufficiently pronounced to maintain the cline despite the homogenizing effect of gene flow (Antoniazza *et al.*, 2010). This raises the question of whether the pronounced variation in coloration found in Central Europe, where dark, pale and intermediately reddish individuals are found, is a consequence of dark birds emigrating from northern Europe and of white birds emigrating from southern Europe; and/or whether it is the consequence of the different colour morphs being adapted to the specific local environmental conditions found in Central Europe. Although gene flow is likely to play an important role in the maintenance of colour polymorphism in Central

Europe, a role of local adaptation in the centre of the cline, where variation in coloration is most pronounced, was also suggested by a recent study carried out in Switzerland. Compared to pale-reddish females, dark-reddish females bred in territories featuring more arable fields, where the latter had higher reproductive success than the former (Dreiss *et al.*, 2011). Nonrandom habitat distribution may explain why dark individuals consume more voles than their paler conspecifics, which eat more wood mice (Roulin, 2004b). Whether these morph-specific adaptations are the result of selective processes having taken place in Europe, or whether they are colour-specific characteristics typical to this species, remains an open question. In other words, the key issue raised here is whether the results found in Europe are specific to that continent as a result of the specific European demographic history (i.e. allopatric evolution followed by interbreeding) or whether the same holds true in other worldwide-distributed barn owl populations independent of similar demographic events (i.e. sympatric evolution of morph-specific characteristics; Roulin, Wink & Salamin, 2009).

To determine whether colour-specific habitat distribution, diet, and morphology are not restricted to Europe but may be a general property of the worldwide-distributed barn owl, we also need to study whether coloration is associated with the way that owls exploit their habitat and diet outside of Europe. In the present study, we report such a study performed in the Middle East where the subspecies *Tyto alba erlangeri* is found. If the results acquired in Switzerland (Dreiss *et al.*, 2011) are applicable also to non-European populations, we suggest two predictions for barn owls from the Middle East: (1) we expect dark-reddish birds to breed in sites where open fields are more frequently found than in sites occupied by lighter coloured individuals and (2) we expect dark-reddish birds to consume more rodents of the family Cricetidae and lighter coloured birds more rodents of the family Muridae. Because colour-specific habitat distribution and diet may require specific morphological adaptations (Roulin & Wink, 2004), we also investigated whether body size is correlated with pheomelanin-based coloration. Based on the finding that dark-reddish Swiss barn owls are longer-tailed (Roulin, 2006), we predicted that, in the Middle East, the degree of pheomelanism would be positively correlated with body size. Our study is of importance beyond its relation to the barn owl in that it emphasizes that patterns of local adaptation found in one population can apply to other populations, located thousands of kilometres away. Furthermore, it suggests that covariation between phenotypic traits such as coloration and foraging habits can evolve in sympatry.

MATERIAL AND METHODS

STUDY AREA AND HABITAT

In spring 2011 we performed a study on barn owls in three major valleys in the north of Israel used for agriculture: Hula Valley (33°07'N, 35°35'E; 55.2% arable fields, 15.8% non-arable fields, 22.9% orchard/plantation, 0.8% urban, 3.5% forest, 1.8% pond/stream); Beit Shean Valley (32°30'N, 35°30'E; 45.6% arable fields, 16.1% non-arable fields, 26.3% orchard/plantation, 5.4% urban, 3.0% forest, 3.6% pond/stream); and Jezreel Valley (32°38'N, 35°18'E; 48.6% arable fields, 12.2% non-arable fields, 23.9% orchard/plantation, 6.7% urban, 6.9% forest, 1.7 pond/stream). Arable fields are similar between the regions and comprise mostly fodder (wheat, sweet corn, alfalfa, clover, vetch, and oats); grain crops and seeds (wheat and sweet corn); and spices and herbs (oregano, hyssop, basil, and dill). Because a previous study revealed that barn owls forage close to their nest (i.e. 90% time within 500 m; Y. Motro, pers. comm.), just before the breeding season, in the present study, we estimated the proportion of the habitat for a 300 m radius around each nest-box that comprised arable fields (wheat, alfalfa, corn, other crops), which represented, on average, 46.8% (range 0–100%). The frequency of the proportions of arable fields reflected an approximately normal distribution.

CAPTURE OF ADULTS

We captured 97 breeding barn owl females and 23 males in nest-boxes (width 50 cm, length 75 cm long, height 50 cm) fixed on poles. For 92 of them, we could determine the laying date as the date when the first egg was laid (mean 27 March, range 7 February to 23 May). We noted the time of the day when we weighed females to the nearest gram (mean 372 g; range 305–450 g), and the number of days between weighing females and the day on which they laid their first egg (mean 48 days; range 4 and 78 days; referred to as 'reproductive stage'). One investigator (M.C.) measured one of their wings (mean 300 mm; range 283–316 mm) and central tail feather (mean 116 mm; range 103–127 mm) to the nearest mm, and the length of their tarsus (mean 77.4 mm; range 70.2–89.7 mm) and beak (mean 19.3 mm; range 15.0–22.6 mm) to the nearest 0.1 mm. Twenty birds ringed the previous year as nestlings were referred to as 'yearling', and 22 other birds ringed as breeders in previous years or as nestlings in 2009 or earlier were denoted 'adult'.

ASSESSMENT OF PLUMAGE TRAITS

To assess pheomelanin-based coloration, we collected three feathers from the breast, belly, flank, and the

underside of one wing. At the end of the breeding season, one investigator (O.P.) took a digital picture (Nikon D300 camera) of the feathers when blinded to the identity of the birds from which these feathers had been taken. Using the digital photography software HIRUNDO (Signal and Image processing Laboratory, Department of Electrical Engineering of the Technion; Vortman *et al.*, 2011), a measure of RGB colour was obtained. In addition to pheomelanin-based coloration, barn owls also vary in the degree of eumelanin-based coloration in the form of black spots located at the feather tips. A 60 × 40 mm frame was placed on the same four body parts, within which eumelanin spots were counted and, their diameter was measured to the nearest 0.1 mm. Mean number of spots (37 spots; range: 15 and 64) and mean spot diameter (1.6 mm; range: 0.7 and 2.8) were calculated and used in the statistical analyses. We did not consider the intensity of spot darkness because spots are lighter coloured when feathers are older, implying that this parameter depends on the degree of feather abrasion. Because females breeding in the three regions (Hula Valley, Beit Shean Valley and Jezreel Valley) did not differ in plumage pheomelanin-based coloration and the number and size of black spots [one-way analysis of variance (ANOVA), $P > 0.41$], we did not include regions in the statistical analyses.

The subsequent analyses validate our method of assessing plumage colouration as reliable and representative of overall coloration. First, as in a recent study (Dreiss & Roulin, 2010), we found that yearling birds were darker-reddish than older adults and that females were darker-reddish than males (two-way ANOVA: $F_{1,51} = 7.92$, $P = 0.007$ and $F_{1,51} = 5.92$, $P = 0.019$). Second, coloration measured on the four different body parts was correlated (Pearson's correlation coefficients $0.37 > r > 0.57$, P -values < 0.0001). Third, as found in Switzerland (Roulin, 2004c), pheomelanin-based coloration was positively correlated with mean spot diameter in males ($r = 0.38$, $n = 30$, $P = 0.037$) but not in females ($r = 0.05$, $n = 111$, $P = 0.58$). Fourth, as in Switzerland (Roulin, 2004c), birds were on average darker coloured on the breast than belly (paired t -test: $t_{123} = 4.77$, $P < 0.0001$).

DIET ANALYSIS

Because, in the barn owl, the female parent starts to help her partner in foraging for the progeny once the offspring are approximately 3 weeks of age (fledging takes place 5–7 weeks later) (Roulin, 2002), it is preferable to collect pellets at the end of the breeding season to study the covariation between female plumage traits and offspring diet. After nestlings had definitely left their nest site, 11 pellets were collected from each of 74 nest-boxes in which at least one

nestling had fledged to analyse diet by identifying mandibles, skulls, and femurs of prey remains. We identified, on average, 26 prey items per nest (range 15–40). We found 751 house mice (*Mus musculus*) (38.6%), 572 social voles (*Microtus socialis guentheri*) (29.4%), 433 Tristram's jirds (*Meriones tristrami*) (22.3%), 21 common rats (*Rattus rattus*) (1.1%), three mole rats (*Heterocephalus glaber*) (0.2%), 118 shrews (*Crocidura* sp.) (6.1%), 24 birds (1.2%), five insects (0.3%), and 19 unidentified small mammals (1.0%). Square-root transformation of the proportion of each prey species normalized the frequency distribution of voles, jirds and mice but not of rats, shrews, and birds. We thus applied nonparametric analysis for the latter three species. To confirm our estimates of diet as reliable, for ten sites, we compared percentages obtained by analyzing 11 pellets with the percentages obtained with 39 supplementary pellets. Percentages obtained with 11 and 50 pellets were very similar for the house mice (Pearson's correlation: $r = 0.81$, $n = 10$, $P = 0.004$), social voles ($r = 0.96$, $n = 10$, $P < 0.0001$), and Tristram's jirds ($r = 0.93$, $n = 10$, $P = 0.0001$).

STATISTICAL ANALYSIS

Two-tailed multiple regression analyses and correlations were carried out using JMP software (Sall & Lehman, 1996). We performed backward model selection using $P = 0.05$ as the threshold value for elimination. Residuals from all models were normally distributed. Because all measurements (i.e. body mass and size, habitat type, and coloration) were not taken in all individuals, the degrees of freedom can vary between analyses.

RESULTS

COLOUR-SPECIFIC HABITAT DISTRIBUTION

In a multiple regression analysis including wing length, laying date, and pheomelanin-based coloration, only the latter variable was significantly associated with the area of arable fields around nest-boxes (colour: $F_{1,94} = 5.72$, $P = 0.019$; wing length: $F_{1,92} = 1.24$, $P = 0.27$; laying date: $F_{1,86} = 0.05$, $P = 0.83$). Dark females bred in sites with more arable fields than did lighter coloured females (Fig. 1A). Laying date tended to be associated with female coloration but not in interaction with the area of arable fields (multiple regression analysis, colour: $F_{1,90} = 3.73$, $P = 0.057$, darker females tended to breed later in the season than lighter coloured individuals; arable fields: $F_{1,88} = 0.36$, $P = 0.55$; interaction: $F_{1,87} = 0.12$, $P = 0.73$).

When considering only the subset of individuals of known age, the area of arable fields around nest-boxes was not associated with age but tended to

be associated with pheomelanin-based colour (multiple regression analysis: $F_{1,38} = 0.94$, $P = 0.34$ and $F_{1,39} = 3.51$, $P = 0.069$). As found in Switzerland, eumelanin-based traits (i.e. the number and size of black spots) were not significantly associated with the area of arable fields ($P > 0.30$).

COLOUR-SPECIFIC DIET

Because the proportions in the diet of the voles, jirds, mice, rats, and birds were not associated with the proportion of arable fields (Pearson's correlations, all P -values > 0.22), we did not consider habitat in the subsequent analyses. Pheomelanin-based coloration was positively correlated with the proportion of social voles in the diet ($r = 0.31$, $n = 74$, $P = 0.008$; Fig. 1B) and negatively with the proportion of Tristram's jirds ($r = -0.29$, $n = 74$, $P = 0.012$) but not with the proportions of mice ($r = -0.12$, $n = 74$, $P = 0.33$), shrews (Spearman's correlation: $r_s = 0.04$, $n = 74$, $P = 0.76$), rats ($r_s = -0.05$, $n = 74$, $P = 0.70$), and birds ($r_s = 0.06$, $n = 74$, $P = 0.62$). To further analyse diet in relation to coloration, we only considered voles and jirds. In a multiple regression analysis, the square-root transformed proportion of voles was significantly associated with date ($F_{1,71} = 17.27$, $P < 0.0001$; more voles were captured at the end than beginning of the season) and coloration ($F_{1,71} = 4.42$, $P = 0.039$) but not with female wing length ($F_{1,69} = 1.40$, $P = 0.24$). In another multiple regression analysis, the square-root transformed proportion of jirds was no longer associated significantly with coloration ($F_{1,69} = 1.88$, $P = 0.18$) but with date ($F_{1,74} = 18.83$, $P < 0.0001$; more jirds were captured at the beginning than end of the season) and wing length ($F_{1,74} = 5.24$, $P = 0.025$; Fig. 2).

Using the subsample of birds of known age, the proportion of voles in the diet was significantly associated with female pheomelanin-based coloration and date but not with female age (multiple regression analysis: $F_{1,29} = 9.16$, $P = 0.005$; $F_{1,29} = 10.14$, $P = 0.004$; $F_{1,28} = 1.50$, $P = 0.23$). In addition, the proportion of jirds in the diet was significantly associated with coloration and date but not with age (multiple regression analysis: $F_{1,29} = 4.53$, $P = 0.04$; $F_{1,29} = 13.53$, $P = 0.001$; $F_{1,28} = 0.008$, $P = 0.93$). As in Switzerland, eumelanin-based traits (i.e. number and size of black spots) were not significantly associated with diet ($P > 0.18$).

RELATIONSHIP BETWEEN COLORATION AND BODY SIZE

To obtain an index of female body size, we extracted the first two components of a principal components analysis, including wing length (loading for the first component is 0.62 and for the second component

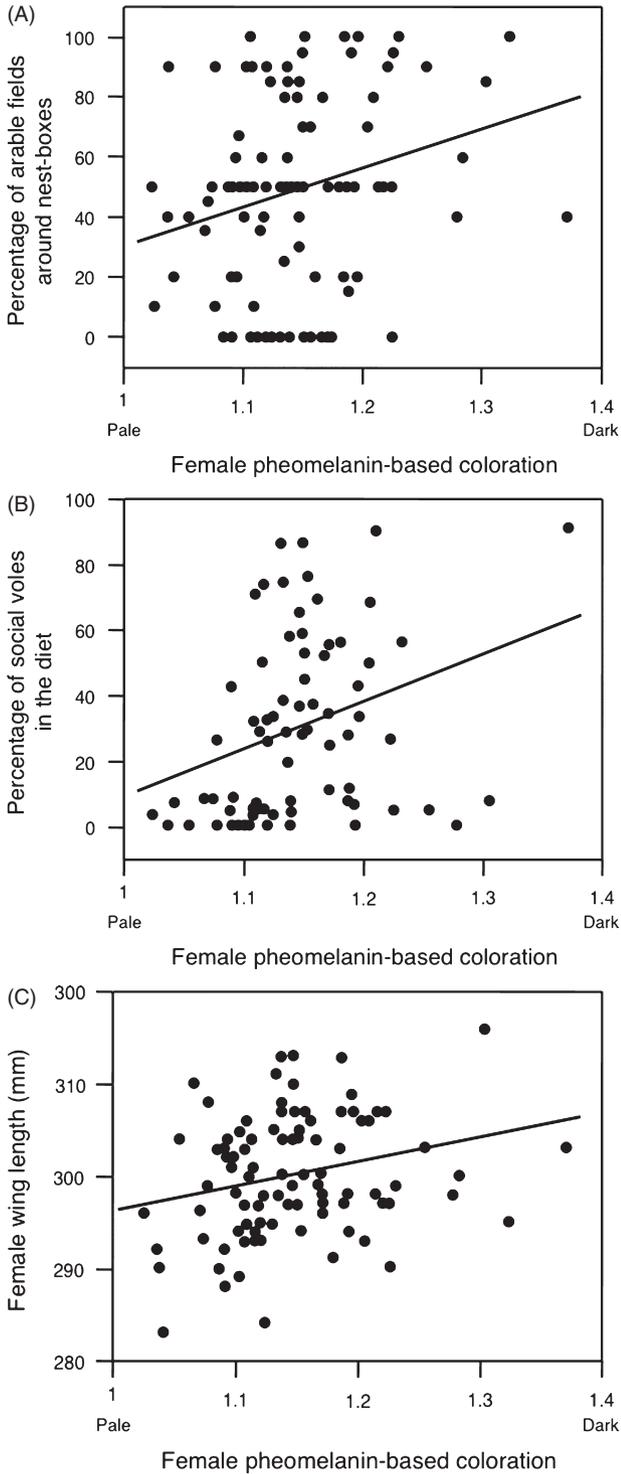


Figure 1. Relationship between pheomelanin-based coloration in female barn owls and (A) the proportion of arable fields around nest-boxes, (B) proportion of social voles in the diet, and (C) female wing length. Regression lines are drawn for illustrative purposes. Spearman's correlations are (A) $r_s = 0.25$, $n = 96$, $P = 0.016$, (B) $r_s = 0.42$, $n = 74$, $P = 0.0002$, and (C) $r_s = 0.25$, $n = 96$, $P = 0.016$, respectively. In (B), the relationship remains significant on removing the darkest individual ($r_s = 0.40$, $n = 73$, $P = 0.0004$).

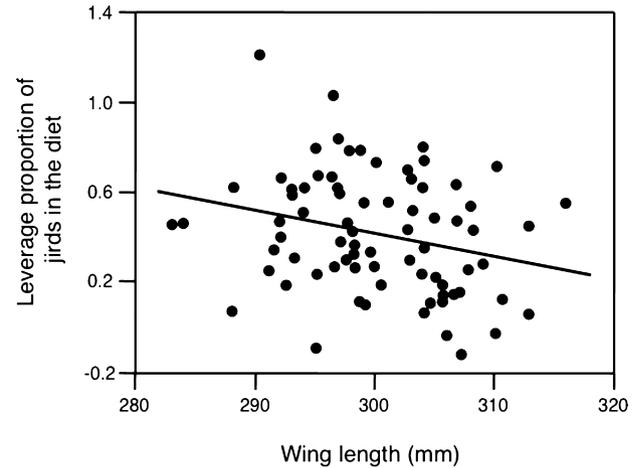


Figure 2. Relationship between wing length and Box-Cox transformed proportion of jirds (*Meriones tristrami*) in the diet of female barn owls. We present leverage from the multiple regression analyses given in the results, including wing length and date as the dependent variables.

-0.28), tarsus length (0.42, 0.32), tail length (0.65, -0.15), and bill length (0.15, 0.89). The eigenvectors for the first and second principal components are, respectively, 1.65 and 1.02 (each component explains 41.2% and 25.5% of the variance in body measures or morphology). Although the first principal component

of female body size was correlated with pheomelanin-based coloration (Pearson's correlation: $r = 0.23$, $n = 91$, $P = 0.03$), the second component was on the borderline of significance ($r = -0.20$, $n = 91$, $P = 0.06$). Darker females had longer wings (Fig. 1C) and tails but shorter bills. The significant relationship between wing length and coloration was not inflated by age because it remained significant after controlling statistically for age using the subsample of birds of known age (two-way ANOVA, coloration: $F_{1,40} = 4.50$, $P = 0.04$; age: $F_{1,39} = 3.00$, $P = 0.09$).

Body mass was not related to plumage coloration after controlling for laying date, wing length and reproductive stage [i.e. the number of days between weighing females and the day on which they laid their first egg (multiple regression analysis: colour: $F_{1,86} = 1.03$, $P = 0.31$; laying date: $F_{1,91} = 1.32$, $P = 0.25$; wing length: $F_{1,92} = 1.45$, $P = 0.23$; reproductive stage: $F_{1,94} = 31.80$, $P < 0.0001$)]. Eumelanin-based traits (i.e. number and size of black spots) were not significantly associated with body size and body mass ($P > 0.23$).

DISCUSSION

The present study shows that dark pheomelanin female barn owls breed in territories where arable fields are more abundant than do their paler conspecifics. More voles are delivered to the offspring when the mother is dark-reddish and more jirds when she is lighter coloured; and, finally, dark birds are longer-winged and longer-tailed than lighter coloured birds. These findings are strikingly similar to those obtained in Switzerland (Roulin, 2004b, 2006; Dreiss *et al.*, 2011).

COLOUR-SPECIFIC HABITAT DISTRIBUTION

Nonrandom habitat distribution with respect to coloration, colour-specific diet, and body size strongly suggests that pheomelanin-based coloration plays a role in foraging. The barn owl is highly variable in pheomelanin-based coloration both within and among populations in most regions in the world (Roulin *et al.*, 2009). Hence, the finding of similar results in both the Middle East and Europe (Dreiss *et al.*, 2011) allows us to hypothesize that pheomelanin-based coloration is associated with foraging strategies in most barn owl populations. This is an important finding because it points to a potential role of predator–prey relationships in the maintenance of variation in pheomelanin-based coloration, both within and among populations on a large geographical scale. Assuming that differently coloured individuals are adapted to alternative habitats and that environmental heterogeneity is temporarily stable, owls may actively search for the breeding sites most suitable for their coloration. Matching habitat choice (Edelaar *et al.*, 2008) would allow birds to breed more successfully in their locally adapted habitat (Ravigné *et al.*, 2004).

COLOUR-SPECIFIC DIET

Why are more small mammals of the family Cricetidae delivered to the nest when the mother is dark-reddish and more prey items of the family Muridae when she is lighter-reddish? Four hypotheses are offered to account for this observation. First, if pairing with respect to coloration is assortative, a relationship between female coloration and diet would be the result of a correlation between male coloration and diet. This is unlikely because the few pairs for which we had data on male and female coloration did not reveal any tendency to assortative pairing ($r = 0.16$, $n = 18$, $P = 0.52$), as already found in Switzerland (Dreiss *et al.*, 2011) and in Hungary (Mátics *et al.*, 2002). Second, because dark- and light-reddish females are located in different habitats, both the female and male parents may have access primarily

to voles when the female is dark-reddish and to jirds when she is lighter-reddish. Although, when testing for a relationship between coloration and diet, we controlled statistically for habitat, we cannot exclude that this relationship is the result of a habitat variable that we did not measure. Third, hunting success on voles and jirds may be colour-specific in females; this hypothesis is reinforced in that we collected pellets after a long period during which the females also participated in food provisioning. For example, the different colour morphs of the barn owls may be a response to the different defensive behaviours employed by Cricetidae and Muridae to avoid predators, which may stem from the rodents' different habitats and motoric abilities (Edut & Eilam, 2003). Even though both the rodents in the present study inhabit farmland, their microhabitats vary: Cricetidae, which have shorter legs and ears, mostly inhabit open landscape or ditches, running in between burrows; whereas Muridae, which have longer ears and legs, forage more on the borders of fields. It is possible that voles detect dark-reddish barn owls less rapidly than light-reddish ones, whereas the reverse is the case with respect to jirds, if the different morphs help to camouflage the owls in the different microhabitats. This hypothesis needs to be tested experimentally by measuring the activity of voles and jirds in the presence of either a dark-reddish or light-reddish owl. Fourth, differential predation upon voles and jirds by dark and light barn owls may be the result of a morphological trait that is correlated to pheomelanin-based coloration. Indeed, we found that dark females are longer-winged and longer-tailed than light-coloured females. The observation that wing length rather than coloration predicts the proportion of jirds provisioned to the progeny suggests that a relationship between coloration and diet is not necessarily caused by variation in coloration itself. Edut & Eilam (2003) found that Cricetidae (social voles) freeze in the presence of barn owls, whereas Muridae (e.g. Tristram's jirds) try to flee. Tristram's jirds are fast agile prey compared to voles, and shorter wings may be advantageous in capturing such prey (Vanhooydonck *et al.*, 2009). More studies are needed to understand why pheomelanin-based coloration is associated with diet.

RELATIONSHIP BETWEEN COLORATION
AND BODY SIZE

In Switzerland, the association between tail length and pheomelanin-based coloration was a result of nonrandom mating, with darker-coloured males having mated with longer-tailed females (Roulin, 2006). In the Middle East, we do not yet have sufficient data to determine whether the association

between coloration and wing and tail length is also a result of nonrandom mating, or whether other genetic mechanisms are responsible for the linkage disequilibrium between these phenotypic traits.

CONCLUSIONS

The present study shows that the findings obtained in two barn owl populations, in Europe and in the Middle East, reflect the same patterns of local adaptation. Further data are needed to establish why dark- and light-reddish owls exploit alternative ecological niches, whether these patterns are applicable to other populations; and, finally, whether the same patterns prevails in other species showing variation in pheomelanin coloration.

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