

Local adaptation and matching habitat choice in female barn owls with respect to melanic coloration

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Abstract

Local adaptation is a major mechanism underlying the maintenance of phenotypic variation in spatially heterogeneous environments. In the barn owl (*Tyto alba*), dark and pale reddish-pheomelanic individuals are adapted to conditions prevailing in northern and southern Europe, respectively. Using a long-term dataset from Central Europe, we report results consistent with the hypothesis that the different pheomelanic phenotypes are adapted to specific local conditions in females, but not in males. Compared to whitish females, reddish females bred in sites surrounded by more arable fields and less forests. Colour-dependent habitat choice was apparently beneficial. First, whitish females produced more fledglings when breeding in wooded areas, whereas reddish females when breeding in sites with more arable fields. Second, cross-fostering experiments showed that female nestlings grew wings more rapidly when both their foster and biological mothers were of similar colour. The latter result suggests that mothers should particularly produce daughters in environments that best match their own coloration. Accordingly, whiter females produced fewer daughters in territories with more arable fields. In conclusion, females displaying alternative melanic phenotypes bred in habitats providing them with the highest fitness benefits. Although small in magnitude, matching habitat selection and local adaptation may help maintain variation in pheomelanin coloration in the barn owl.

Introduction

Understanding how phenotypic diversity persists within populations is a key goal in evolutionary biology. Spatial and temporal fluctuation in environmental conditions within populations can account for the long-term coexistence of phenotypic variants (Kassen, 2002; Bell, 2010). Local adaptation as a mechanism to maintain phenotypic variation has received theoretical and empirical support coming mainly from the botanic literature, animals of economic value, host–parasite interactions and laboratory studies (Galloway & Fenster, 2000; Kawecki & Ebert, 2004; Parker & Gilbert, 2004; Garcia de Leaniz *et al.*,

2007; Laine & Tellier, 2008). Studying local adaptation in genetically colour polymorphic species is promising because colour morphs can be cryptic in different habitats (Endler, 1984; Stuart-Fox *et al.*, 2004), and they are often associated with specific physiological and behavioural adaptations (Forsman *et al.*, 2002; Ducrest *et al.*, 2008). Heterogeneous environments can act as divergent selective force either directly on coloration or indirectly on genetically correlated traits. For this reason, the potential is high that individuals displaying alternative colour morphs are adapted to different habitats (e.g. Hoekstra *et al.*, 2005; Sirkia *et al.*, 2010).

In species showing clinal variation with one phenotype being adapted to conditions found at one extreme part of an environmental gradient and another phenotype at the other extreme part, it is not obvious whether the two phenotypes and their hybrids can find habitats where they are adapted in the central part of the gradient (e.g.

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Storz & Dubach, 2004; Dionne *et al.*, 2008; Montague *et al.*, 2008). Local adaptation may explain the occurrence of different phenotypes at the extreme parts of a gradient, whereas phenotypic variation in the centre of the gradient may be maintained by gene flow due to migration from the different locations along the gradient (Barton & Hewitt, 1985). Alternatively, if in the centre of the gradient the different phenotypes can find habitats where they are locally adapted, individuals may disperse to find the best conditions to which they are adapted. This so-called 'matching habitat choice' would help maintain local adaptations (Edelaar *et al.*, 2008).

In numerous animals, colour polymorphism is due to differential deposition of melanin pigments. For instance, in the barn owl (*Tyto alba*), heritable pheomelanin coloration (in Switzerland $h^2 = 0.81$, Roulin & Dijkstra, 2003) varies continuously from pale (i.e. white) to dark reddish pheomelanin. On the European continent, clinal variation is extremely pronounced, with individuals being mostly reddish in North-Eastern and whitish in South-Western Europe, whereas in Central Europe colour variation is extensive (Roulin *et al.*, 2009). A recent study that compared the magnitude of differentiation in coloration (P_{ST}) with that of neutral genetic markers (F_{ST}) showed that reddish owls are adapted to environmental conditions prevailing in North-Eastern Europe and whitish owls to conditions found in South-Western Europe. Greater differentiation in coloration than at neutral genetic markers suggests that selection exerted on coloration or on genetically correlated traits overcomes the homogenizing effect of gene flow (Antoniazza *et al.*, 2010). It remains unclear whether the extreme level of colour variation found in Central Europe is due to gene flow and the interbreeding of reddish and whitish individuals and/or whether the different colour phenotypes are adapted to specific local conditions. Understanding the interaction between phenotype and environment at this local scale is crucial to foresee the importance of anthropologic effects like agricultural practice and deforestation. Both in allopatry (i.e. in North-Eastern and South-Western Europe) and in sympatry (i.e. in Switzerland), reddish individuals consume more voles than whitish individuals that eat more mice (Roulin, 2004a). This suggests that these two extreme colour morphs specialize on different prey species or that they occupy different habitats.

In a barn owl population located in Central Europe, we tested different predictions of the hypothesis that reddish and whitish phenotypes are adapted to different habitats. (i) *Plumage-specific habitat selection*. We predict that owls breeding in different years in the same territory resemble each other with respect to pheomelanin-based coloration. We also tested whether the association between colour and breeding site could be due to coloured individuals breeding preferentially in some habitats and moving from one site to another according to their environmental characteristics. (ii) *Territory-specific repro-*

ductive parameters of plumage phenotypes. We expect reproductive success to be higher when the focal individual breeds in habitat which is usually used by its colour phenotype. We also predict brood sex ratio to be biased towards the sex adapted to the environmental characteristics found in the breeding territory. (iii) *Plumage-specific adaptations to rearing conditions*. We expect that nestlings are also adapted to habitat which is usually used by their parents' colour phenotype. We therefore tested whether rearing conditions prevailing in nests of parents of a given coloration are better suited to nestlings born from similarly rather than dissimilarly coloured parents. To this end, we analysed growth rate of nestlings that had been previously swapped at hatching between randomly chosen nests. Cross-fostering experiments are appropriate to investigate whether there is an interaction between phenotype and environment. Testing these predictions will allow us to discuss the extent to which spatial environmental heterogeneity may facilitate the maintenance of phenotypic variation in the central part of a geographic cline such as the one found for melanin-based coloration in the European barn owl.

Methods

General method

The study was carried out in western Switzerland (46°49'N/06°56'E) in a study area of 190 km² where 196 nest-boxes (1.0 × 0.6 × 0.5 m) have been fastened against barn walls, among which 141 have been occupied by at least one breeding pair, between 1994 and 2010. The barn owl is a medium-sized (females weigh on average 367 g) nocturnal raptor that primarily feeds upon small mammals captured in open landscapes. Barn owls are mostly monogamous with very little extra-pair paternity (Roulin *et al.*, 2004). In our Swiss study area, birds lay between 2 and 11 eggs (mean ± SE of 936 clutches that gave at least one nestling laid between 1990 and 2010: 6.1 ± 1.6) from 23th of February to 6th of August (mean ± SE of 1087 clutches: 29th of April ± 24 - days) and brood size at fledging ranges from 1 to 9 (mean ± SE of 943 broods that produced at least one fledgling: 4.2 ± 1.4). In 10 years (1996, 1998, 2000, 2001, 2002, 2004, 2007, 2008, 2009 and 2010), we performed partial cross-fostering experiments by exchanging approximately half of the hatchlings between pairs of nests with the criterion that broods had a similar hatching date (mean difference in hatching date of the first laid egg of the two nests of a same pair ± SE: 4 ± 3 days). In 3 years (1999, 2003 and 2006), we carried out a full cross-fostering experiment by swapping clutches between pairs of nests (Roulin *et al.*, 2001). In 1994, 1995, 1997 and 2005, no cross-fostering experiment was performed. A blood sample was taken to determine nestling sex from blood cell DNA using sex-specific molecular markers (Roulin *et al.*, 1999).

Assessment of melanin-based plumage traits

As on each body part, feathers are all similarly coloured, A. Roulin compared pheomelanin-based coloration on the breast, belly, one flank and the underside of one wing with eight colour chips ranging from I for reddish to VIII for white. For each individual, these four values were averaged and used in the statistical analyses. As already demonstrated, coloration scored by eye in the field is strongly correlated ($r = -0.73$) with reflectance in the range 400–700 nm measured with an Ocean Optics S2000 spectrometer and a PX-2 xenon lamp (Ocean Optics Inc., Duiven, the Netherlands; Dreiss & Roulin, 2010). Because we have more data on coloration scored in the field than with a spectrometer, we performed statistical analyses on the former values (nevertheless, we performed all analyses also on reflectance data and found qualitatively similar results). Barn owls vary not only with respect to pheomelanin-based coloration but also eumelanin-based coloration in the form of black spots located at the tip of feathers. A 60×40 mm frame was placed on the same four body parts within which eumelanin spots were counted and their diameter measured to the nearest 0.1 mm. Mean number of spots and mean spot diameter were calculated and used in the statistical analyses. Reliability of assessing plumage traits has already been demonstrated elsewhere (Roulin, 1999, 2004d). 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.

Assessment of habitat characteristics

Habitat characteristics were assessed in spring 2009 within an area around all nest sites defined by radiuses of 1.0 km (for further details see Frey *et al.*, 2011). This area corresponds to the mean home range of breeding males in our study area (Arlettaz *et al.*, 2010). The landscape classification was made with a Geographic Information System software (ArcGIS 9.2; Environmen-

tal Systems Research Institute, Inc., Redlands, CA, USA), using aerial images (0.5 m resolution) to identify the structural features of the habitat. In total, four habitat classes were defined: altitude where the nest-box was fixed, wood area, arable field and meadow area and urban/suburban area. Meadow includes intensive meadow (fertilized grassland that is part of the crop rotation) and extensive meadow (nonploughed grassland with cattle). We did not consider water surface, river and swamp because they cover < 5% of the total area for all nest sites. Because habitat characteristics were highly correlated (less wooded sites are higher in altitude, contain less open fields, and less urban area, more open area are lower in altitude and contain less urban area, Table 1), we generated an index of habitat characteristics around each nest site, by performing a principal components analysis on correlation matrix on all variables (Table 1). For the subsequent analyses, we retained the first two components for which eigenvalues were larger than 1, which explained 82% of the variance (Table 1). As can be seen in Table 1, PC1 indicates the extent to which a territory is covered by woods and PC2 by fields.

Statistical procedure

Analyses were computed with the computer program SAS v 9.1 (SAS Institute Inc., Cary, NC, USA). Because each nest-box could be used in more than 1 year, we set site as repeated measurement to account for within-subject variation in our analyses. To account for the between-subject variation of year and breeder identity, we fitted year and identity of breeders as two random factors in analyses, unless specified otherwise. We only consider the first annual breeding attempt, as < 10% of individuals produced two annual clutches. Because plumage coloration and reproductive output fluctuate with age in the population (Dreiss & Roulin, 2010), individual age in years was included as covariate in the analyses. We performed backward model selection using $P = 0.05$ as the threshold value for elimination. Final models only contained significant effects, and main effects involved in

Table 1 Loadings of the variables of habitats on the first two principal components extracted from a principal components analysis including altitude (m), wood area, field or meadow area and urban or suburban area (% of the area of a diameter of 2.0 km) around every 196 nest-boxes. Correlation matrix indicates the Pearson's coefficients between the different variables.

| Habitat variables | Mean \pm SE | Range | Correlation matrix | | | Principal components | |
|-----------------------|---------------|---------|--------------------|-----------------|-------------------|----------------------|-------------|
| | | | Wood | Field or meadow | Urban or suburban | PC1 'Wood' | PC2 'Field' |
| Altitude (m) | 521 \pm 75 | 430–730 | 0.46 | –0.17 | –0.32 | 0.49 | 0.26 |
| Wood (%) | 16 \pm 12 | 0–65 | – | –0.67 | –0.41 | 0.67 | –0.09 |
| Field or meadow (%) | 82 \pm 16 | 25–100 | – | – | –0.23 | –0.46 | 0.65 |
| Urban or suburban (%) | 8 \pm 7 | 0–50 | – | – | – | –0.33 | –0.71 |
| Eigenvalue | | | | | | 2.00 | 1.27 |
| Cumulative variance | | | | | | 0.50 | 0.82 |

significant interactions. Means are quoted \pm SE. More details on the analyses are given below for each specific prediction.

Plumage-specific habitat selection

We performed one-way ANOVA repeatability analyses (Lessells & Boag, 1987) to examine whether same-sex adults producing their first annual clutch in the same site in different years resemble each other with respect to plumage traits. Only the sites occupied by at least two same-sex breeders in different years were included in this analysis. If an individual reproduced several years in the same site, we kept only the first occurrence of the individual in the site, and thus in the dataset, each individual appears only once per site.

Considering individuals that bred in the study area at least during 2 years in a row, we analysed whether the probability of remaining in the same nest site rather than changing site is associated with coloration in interaction with habitat characteristics. The probability of site change from 1 year to the next was analysed with a generalized mixed model with binomial error distribution where year and breeder identity were incorporated as two random factors; individual coloration and habitat characteristics at the first site (i.e. before the decision to change site or not) as well as their interaction were set as covariates. For individuals that changed sites between two consecutive years, we further analysed whether the difference in habitat characteristics between the previous and new site was related to individual plumage traits. Year and breeder identity were set as random factors with differences in habitat PC1 and habitat PC2 as dependent variables in separate mixed models. The mean (\pm SE) distance between the two successive sites for the females that changed sites between two successive years was 3.796 ± 0.316 km (range: 0.413–27 km). In males, the breeding sites were closer, at an average distance of 1.687 ± 0.097 km (range: 0.092–5.115 km).

Territory-specific reproductive success of plumage phenotypes

We analysed reproductive parameters at the first annual breeding attempt in female and male breeders separately. If an individual reproduced several years in the same site, we kept only its first occurrence in the site. Hatching date of the first-hatched offspring and number of fledglings for clutches where at least one nestling fledged were the dependent variable in separate mixed models. Brood sex ratio was analysed with generalized mixed model with female breeder plumage coloration and habitat PC1 and PC2 as covariates. Year and individual identity were included as random factors and site as a repeated factor.

Plumage-specific adaptations to rearing conditions

We used data from cross-fostering experiments gathered in 13 of 17 years. Among pairs of nests used to cross-

foster eggs or hatchlings, breeding females did not significantly resemble each other with respect to pheomelanin-based coloration (Pearson correlation: $r = 0.08$, $n = 296$ pairs of nests, $P = 0.15$). We measured nestlings at the end of the rearing period, that is, between 45 and 65 days after birth, birth date of each individual being determined soon after hatching by measuring wing length (Roulin, 2004c). The relationships between wing length, body mass and age are linear (data not shown). In the case individuals were measured on several occasions, we calculated mean trait values to be used in the statistical analyses so that each nestling appears only once. Age of the nestlings at which they were measured was neither associated with nestling sex ($F_{1,548} = 0.01$, $P = 0.96$) nor with pheomelanin-based coloration of the biological and foster mothers ($F_{1,548} = 0.01$, $P = 0.96$ vs. $F_{1,548} = 0.11$, $P = 0.74$) or with habitat characteristics (PC1: $F_{1,548} = 0.05$, $P = 0.83$ vs. $F_{1,548} = 0.29$, $P = 0.59$). We performed two mixed-model ANCOVAs, one for wing length and another for body mass entered as dependent variables. Because siblings sharing the same nest are not statistically independent, nest identity was entered as a random factor nested in year. Site was set as a repeated factor. We incorporated the term nestling sex as independent factor because nestling females are heavier and bigger than nestling males (Roulin *et al.*, 1999) implying that one sex may be more sensitive to variation in rearing conditions than the other sex.

Results

Plumage-specific habitat selection

Females breeding in the same nest site in different years resembled each other with respect to pheomelanin-based coloration [repeatability = 0.10 ± 0.04 ; $F_{113,442} = 1.51$, $P = 0.0017$; for 114 different sites and 434 different female breeders, with on average 6.4 (SD = 2.8; range: 2–13) different females per site, Fig. 1], but not with respect to number spots or spot diameter (P -values > 0.12). This result was not blurred by female age because different breeding females captured in the same site were not necessarily similarly aged ($F_{113,433} = 1.00$, $P = 0.48$). Furthermore, when considering only females older than 1 year (birds become whiter between the first- and second-year of age), the repeatability was still significant (0.16 ± 0.08 ; $F_{94,160} = 1.40$, $P = 0.032$). To investigate whether these significant repeatability values arose because philopatric males that changed mate are consistently pairing with similarly coloured partners, we compared pheomelanin-based coloration of females breeding at the same site with different males: they were similarly coloured (only the first occurrence of each male in a site was retained: repeatability for female coloration = 0.11 ± 0.05 ; $F_{112,255} = 1.41$, $P = 0.013$), suggesting that similarly coloured females selected the same sites independently of male mate choice.

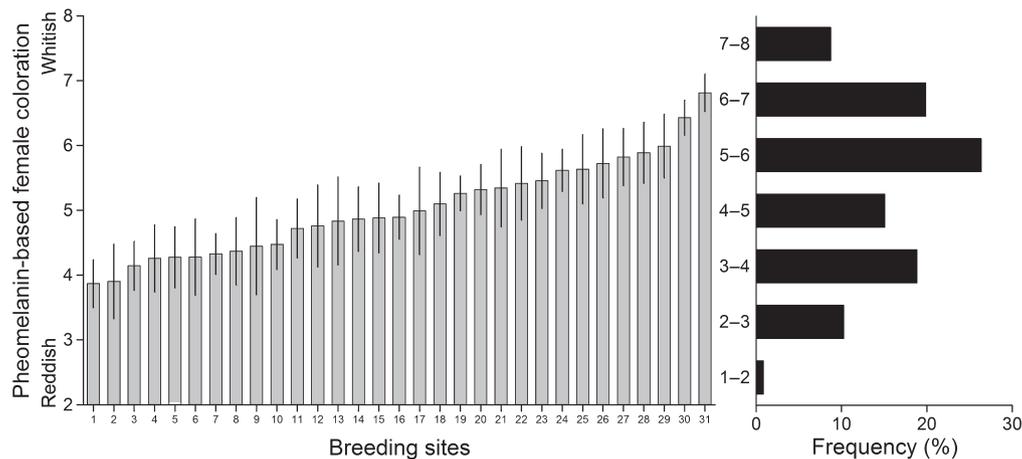


Fig. 1 Plumage-specific habitat selection. Mean pheomelanin-based coloration of female barn owls breeding in the same nest site between 1994 and 2010. Each bar represents the mean (\pm SE) coloration of all individuals that bred in a given site. In this figure (but not in the analyses), only the 31 sites most occupied are represented (at least seven different female breeders). It shows that in some sites, most females are dark reddish, and in others they are usually intermediately coloured, whereas in other sites most females are whitish. The right panel indicates the frequency distribution (in %) of pheomelanin-based coloration of female breeders in the population.

We investigated whether the major environmental components of a barn owl territory (i.e. forests vs. fields) explain the nonrandom distribution of females with respect to coloration. Accordingly, pheomelanin-based coloration of female breeders was related to the interaction between female age and the second principal components of habitat characteristics PC2 (Table 2). Other variables (PC1, geographic coordinates) were not significantly associated with female coloration (Table 2). For females older than 1 year, pheomelanin-based coloration significantly decreased with PC2 (-0.23 ± 0.05 , $F_{1,37} = 18.30$, $P = 0.0001$, Fig. 2), whereas the plumage

Table 2 Plumage-specific habitat selection. Mixed-model ANCOVA testing in the barn owl the relationship between female pheomelanin-based coloration and habitat characteristics, with female identity ($N = 441$) and year ($N = 17$) as random factors and site as repeated factor ($N = 140$). The terms of the final model are written in bold and nonsignificant results of the initial full models in plain.

| Coefficient | Female pheomelanin-based coloration | | | |
|---------------------------------|-------------------------------------|--------------|-------------|-------------------|
| | Estimate \pm SE | <i>F</i> | d.f. | <i>P</i> |
| Intercept | 4.41 \pm 0.09 | 2190 | 1,16 | < 0.001 |
| Habitat PC1 | – | 0.72 | 1,91 | 0.40 |
| Habitat PC2 | 0.03 \pm 0.06 | 0.21 | 1,94 | 0.65 |
| X Swiss coordinate | – | 1.37 | 1,91 | 0.25 |
| Y Swiss coordinate | – | 0.61 | 1,91 | 0.44 |
| Female age | 0.29 \pm 0.03 | 96.41 | 1,94 | < 0.001 |
| Age \times habitat PC1 | – | 2.51 | 1,88 | 0.12 |
| Age \times habitat PC2 | –0.06 \pm 0.02 | 5.91 | 1,94 | 0.017 |
| Age \times X Swiss coordinate | – | 0.14 | 1,88 | 0.71 |
| Age \times Y Swiss coordinate | – | 3.89 | 1,88 | 0.06 |

of 1-year-old females was not significantly related to PC2 ($F_{1,282} = 2.10$, $P = 0.15$, female identity was not fitted as random factor because each female appeared once in this analysis, Fig. 2). This indicates that in old females, darker reddish individuals were located in habitats with more arable fields and meadows than whitish females. Other female plumage traits were not significantly related to any of the two habitat components (P -values > 0.10).

In contrast to females, males breeding in the same nest site in different years did not resemble each other with respect to pheomelanin-based coloration and the two eumelanin-based traits [P -values > 0.54 , for 316 different males breeding in 100 different sites with on average 4.8 (SD = 1.9; range: 2–10) different males per site], and male plumage traits were not significantly related to any of the two habitat components (P -values > 0.14). Coherently, males and females were not assortatively paired by plumage coloration, as male plumage pheomelanin-based coloration was not correlated with coloration of his partner ($F_{1,183} = 1.99$, $P = 0.16$, in a mixed model with the 316 males paired in 569 different pairs, each pair appearing once, with year and male identity as random factors, interactions between habitat and female partner coloration were not significant), confirming previous results obtained with a lower number of pairs (Roulin, 1999).

Females may be constrained in their choice of habitats and hence move from one site to another between years to improve the matching between coloration and habitat. Yet, the probability for 151 females that bred two consecutive years in the study area to quit a breeding site from 1 year to the next was not related to their plumage or to habitat characteristics (coloration:

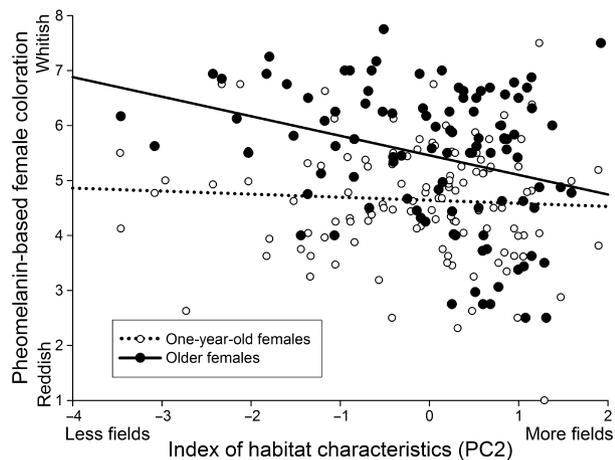


Fig. 2 Plumage-specific habitat selection. Mean pheomelanin-based coloration of female barn owls in relation to an index of habitat characteristics surrounding their nest (PC2) in 1 year old (open circle, average values of 120 sites occupied by 300 different females) and older females (closed circle, average values of 100 sites occupied by 199 different females). Regression lines are drawn for illustrative purpose.

$F_{1,131} = 2.57$, $P = 0.11$, spot diameter: $F_{1,131} = 0.12$, $P = 0.73$, number of spots: $F_{1,131} = 1.50$, $P = 0.22$, PC1: $F_{1,131} = 2.87$, $P = 0.09$, PC2: $F_{1,131} = 0.42$, $P = 0.52$, all P -values of two-way interactions > 0.15 , year and female identity as random factors). However, among the 95 females that changed breeding site from 1 year to the next, we found that whitish individuals settled in more wooded area in the second year compared with the first year; that is, difference in PC1 between the two successive sites was positively related to female coloration ($F_{1,18} = 4.99$, $P = 0.038$, Fig. 3, year and female identity as random factors; other female plumage traits were not related to the difference in PC1: spot diameter: $F_{1,11} = 0.01$, $P = 0.99$, number of spots: $F_{1,11} = 2.18$, $P = 0.17$). The availability of the different habitats did not significantly differ according to females coloration: in the range of female breeding dispersal (3.796 m on average), sites did not differ in PC1 for whitish and reddish females (effect of female coloration on mean PC1 of surrounding sites: $F_{1,41} = 2.65$, $P = 0.11$ in a mixed model with female identity as random factor). Difference in PC2 between the two successive sites was not related to female plumage traits (coloration: $F_{1,11} = 0.11$, $P = 0.74$, spot diameter: $F_{1,11} = 0.17$, $P = 0.69$, number of spots: $F_{1,11} = 1.00$, $P = 0.34$).

Site fidelity within the 140 males that bred two consecutive years in the area was not related to their plumage or habitat characteristics (P -values > 0.13). Among 68 nonphilopatric males, the difference in habitat characteristics between two successive sites was not related to their plumage traits (P -values > 0.19).

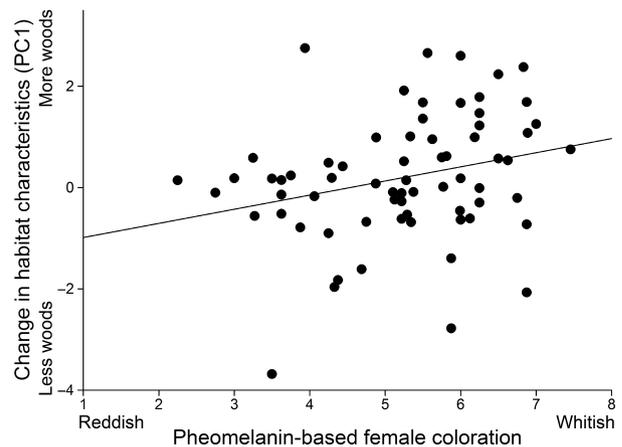


Fig. 3 Plumage-specific habitat selection. Difference in habitat characteristics (PC1) between two successive sites in relation to pheomelanin-based coloration of female barn owls that changed site from 1 year to the next (average values for 79 sites where 95 different females bred). Regression line is drawn for illustrative purpose.

Territory-specific reproductive success of plumage phenotypes

Given that barn owls select breeding sites nonrandomly with respect to their pheomelanin-based coloration, owls may achieve a higher reproductive success when breeding in a site with specific habitat characteristics. The number of fledglings a female produced was related to the interaction between her pheomelanin-based coloration, her age and the habitat PC1 (Table 3). The number of fledglings of females older than 2 years was related to the interaction between her pheomelanin-based coloration and the habitat PC1 ($F_{1,108} = 4.08$, $P = 0.045$, mixed model with year as random factor and site as repeated factors for 98 different females breeding in 70 different sites). In these old female breeders, whitish individuals achieved a higher reproductive success if breeding in a wooded area (high PC1) (Fig. 4). The number of fledglings of yearling females was not related to habitat PC1 alone or in interaction with pheomelanin-based coloration (PC1: $F_{1,212} = 0.47$, $P = 0.49$; PC1* pheomelanin-based coloration: $F_{1,211} = 1.81$, $P = 0.18$, in a mixed model with year as random and site as repeated factors for 319 different females breeding in 117 different sites). Hatching date was not related to habitat characteristics or female plumage coloration (Table 3, for 441 different females breeding in 140 different sites).

If some sites are better suited for some phenotypes in females, we expect that brood sex ratio at birth to be biased differently in different sites. Accordingly, the brood sex ratio was related to the interaction between mother coloration and habitat characteristics PC2 (Table 3). Brood sex ratio was not related to habitat features (PC2: $F_{1,45} = 0.05$, $P = 0.82$), but whitish

Table 3 Territory-specific reproductive success of plumage phenotypes. Mixed-model ANCOVAs testing in the barn owl the relationships between the reproductive parameters (hatching date, number of fledglings) in relation to female pheomelanin-based coloration and habitat characteristics with female identity and year as random factors and site as repeated factor. A similar generalized mixed model was carried out for brood sex ratio (339 different females breeding in 102 different sites). The terms of the final models are written in bold. Sample size for the analysis of hatching date and number of fledglings, respectively: 441 and 381 different females breeding in 140 and 124 different sites.

| Coefficient | Hatching date | | | | Number of fledglings | | | | Brood sex ratio | | | |
|------------------------|-------------------|-------------|-------------|-------------------|----------------------|-------------|-------------|-------------------|---------------------|--------------|-------------|---------------|
| | Estimate ± SE | F | d.f. | P | Estimate ± SE | F | d.f. | P | Estimate ± SE | F | d.f. | P |
| Intercept | 123 ± 5 | 624 | 1,16 | < 0.001 | 3.8 ± 0.4 | 94.0 | 1,16 | < 0.001 | -0.44 ± 0.18 | 5.96 | 1,12 | 0.03 |
| Female age | -1.8 ± 0.6 | 9.69 | 1,90 | 0.0025 | -0.11 ± 0.15 | 0.55 | 1,63 | 0.46 | -0.025 ± 0.031 | 0.64 | 1,45 | 0.43 |
| Female coloration | - | 1.72 | 1,90 | 0.19 | 0.11 ± 0.07 | 2.39 | 1,63 | 0.12 | 0.025 ± 0.035 | 0.52 | 1,45 | 0.48 |
| Habitat PC1 | - | 0.51 | 1,90 | 0.48 | 0.70 ± 0.28 | 6.57 | 1,63 | 0.013 | - | 0.01 | 1,43 | 0.91 |
| Habitat PC2 | - | 0.63 | 1,90 | 0.43 | - | 0.07 | 1,62 | 0.79 | 0.54 ± 0.18 | 9.36 | 1,45 | 0.0037 |
| Age × coloration | - | 0.96 | 1,83 | 0.33 | 0.01 ± 0.03 | 0.32 | 1,63 | 0.57 | - | 0.01 | 1,38 | 0.95 |
| Age × PC1 | - | 2.37 | 1,83 | 0.13 | -0.34 ± 0.12 | 8.13 | 1,63 | 0.006 | - | 1.45 | 1,38 | 0.24 |
| Age × PC2 | - | 3.11 | 1,83 | 0.08 | - | 0.58 | 1,59 | 0.45 | - | 2.33 | 1,38 | 0.14 |
| Coloration × PC1 | - | 0.46 | 1,83 | 0.50 | -0.13 ± 0.05 | 6.47 | 1,63 | 0.013 | - | 1.34 | 1,38 | 0.25 |
| Coloration × PC2 | - | 0.30 | 1,83 | 0.58 | - | 0.11 | 1,59 | 0.74 | -0.11 ± 0.03 | 10.62 | 1,45 | 0.0021 |
| PC1 × PC2 | - | 3.74 | 1,83 | 0.06 | - | 1.02 | 1,59 | 0.32 | - | 0.38 | 1,38 | 0.54 |
| Age × coloration × PC1 | - | 0.27 | 1,81 | 0.60 | 0.06 ± 0.02 | 9.11 | 1,63 | 0.0037 | - | 0.92 | 1,36 | 0.34 |
| Age × coloration × PC2 | - | 0.01 | 1,81 | 0.98 | - | 0.14 | 1,59 | 0.71 | - | 0.53 | 1,36 | 0.47 |

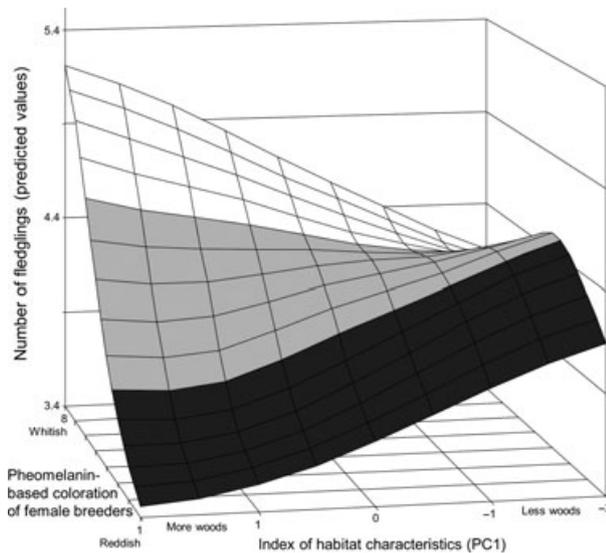


Fig. 4 Territory-specific reproductive success of plumage phenotypes. Number of fledglings produced by old female barn owls (> 2 years old) as a function of their pheomelanin-based coloration and the habitat characteristic PC1. Surface plots are drawn from the predicted values of the final mixed model on the number of fledglings with bivariate spline method for the data set interpolation (Harder & Desmarais, 1972).

females produced fewer daughters when breeding in an area with more fields (Fig. 5).

All analyses for the other female plumage traits (i.e. number and size of black spots) as well as analyses performed on 316 different males breeding in 100 different sites yielded nonsignificant results and are thus not reported.

Plumage-specific adaptations to rearing conditions

Assuming that differently plumaged barn owls select different nest sites because they are adapted to their nestling growth, we predict that nestlings born from parents displaying specific plumage traits grow better if raised by foster parents displaying the same rather than different plumage characteristics. Nestling wing length was related to the interaction between the pheomelanin-based coloration of the foster mother and habitat characteristic PC1 and to the three-way interaction between pheomelanin-based coloration of the biological and foster mothers and nestling sex (Table 4). The first interaction means that nestlings raised by reddish mothers grew smaller wings in wooded area, whereas the opposite trend is true for whitish mothers. The second interaction indicates that daughters had longer wings when biological and foster mothers were both whitish and to a lower extent when they were both reddish (Fig. 6; interaction between the coloration of biological and foster mothers in a similar mixed model on daughters: 0.73 ± 0.36 , $F_{1,164} = 4.11$, $P = 0.044$). In sons, wing length was not related to the interaction between coloration of biological and foster mothers ($F_{1,171} = 0.14$, $P = 0.71$). Similar analyses on nestling body mass were not significant (Table 4).

All analyses for the other female plumage traits (i.e. number and size of black spots) as well as analyses performed on males yielded nonsignificant results and are thus not reported.

Discussion

We found results indicating that females, but not males, displaying a pheomelanin-based coloration trait to

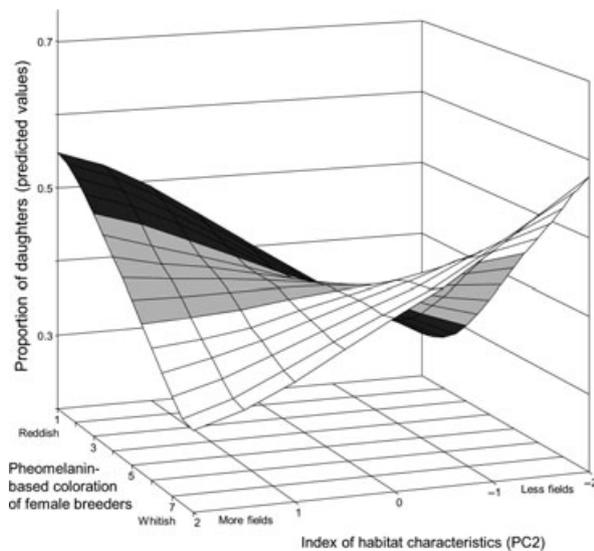


Fig. 5 Territory-specific reproductive success of plumage phenotypes. Proportion of daughters produced by female barn owls as a function of their phaeomelanin-based coloration and the habitat characteristic PC2. Surface plots are drawn from the predicted values of the final mixed model on the number of fledglings with bivariate spline method for the data set interpolation (Harder & Desmarais, 1972).

different extent settled in alternative habitats that better matched their capacities (Table 5): (i) females breeding at the same site in different years were similarly coloured (Fig. 1), old whitish females were located in habitats with less arable fields and meadows than reddish females (Fig. 2) and when whitish females changed breeding site, they settled in more wooded habitats than reddish females did (Fig. 3); (ii) old whitish females produced more fledglings if breeding in a wooded site, whereas the opposite pattern was found in old reddish females (Fig. 4); (iii) whitish females produced fewer daughters when reproducing in habitats with more arable fields and meadows, whereas we found the opposite trend in reddish females (Fig. 5); (iv) female nestlings raised in a foster nest grew their wings more rapidly when their foster and biological mothers were similarly rather than dissimilarly coloured (Fig. 6) and nestlings raised by a reddish foster mother grew longer wings when the habitat surrounding their nest was less wooded.

The nonrandom habitat distribution of phaeomelanin colour morphs among habitats found in our population appears to result from colour-dependent breeding site selection, especially in nonphilopatric females. This could reveal a difference in competitiveness, for instance, if some phaeomelanin morphs are more aggressive and able to acquire preferred habitat (Ducrest *et al.*, 2008). Yet,

Table 4 Plumage-specific adaptations to rearing conditions. Mixed-model ANCOVAs testing in the barn owl the relationship between phaeomelanin-based coloration of foster and biological mothers on offspring wing length (mm) and body mass (g) measured at the end of the rearing period between 45 and 65 days of age with brood nested in year as random factors and site as repeated factor. The terms of the final models are written in bold. Sample size for the analysis of nestling wing length was 995 nestlings from 404 broods.

| Coefficient | Nestling wing length | | | | Nestling body mass | | | |
|--------------------------------------|------------------------------------|----------------|--------------|-------------------|------------------------------------|--------------|--------------|-------------------|
| | Estimate \pm SE | <i>F</i> | d.f. | <i>P</i> | Estimate \pm SE | <i>F</i> | d.f. | <i>P</i> |
| Intercept | 67 \pm 10 | 48.16 | 1,400 | < 0.001 | 423 \pm 13 | 997.3 | 1,416 | < 0.001 |
| Nestling age | 3.5 \pm 0.1 | 1121.87 | 1,544 | < 0.001 | -1.27 \pm 0.26 | 24.12 | 1,563 | < 0.001 |
| Nestling sex | -30 \pm 8 | 13.21 | 1,544 | < 0.001 | -15.2 \pm 1.6 | 88.58 | 1,563 | < 0.001 |
| Coloration of biological mother (Bm) | -2.17 \pm 1.47 | 0.01 | 1,544 | 0.94 | - | 0.06 | 1,546 | 0.81 |
| Coloration of foster mother (Fm) | -1.06 \pm 1.49 | 0.86 | 1,544 | 0.35 | - | 1.16 | 1,546 | 0.28 |
| Habitat PC1 | -4.17 \pm 1.58 | 6.99 | 1,544 | 0.008 | - | 0.99 | 1,546 | 0.32 |
| Habitat PC2 | - | 0.42 | 1,545 | 0.52 | - | 0.65 | 1,546 | 0.42 |
| Sex \times Bm | 4.54 \pm 1.55 | 8.55 | 1,544 | 0.004 | - | 0.14 | 1,539 | 0.71 |
| Sex \times Fm | 4.47 \pm 1.55 | 8.36 | 1,544 | 0.004 | - | 0.11 | 1,539 | 0.74 |
| Sex \times PC1 | - | 2.24 | 1,540 | 0.14 | - | 2.00 | 1,539 | 0.16 |
| Sex \times PC2 | - | 0.27 | 1,540 | 0.60 | - | 0.02 | 1,539 | 0.90 |
| Bm \times Fm | 0.32 \pm 0.27 | 0.04 | 1,544 | 0.83 | - | 0.04 | 1,539 | 0.84 |
| Bm \times PC1 | - | 0.78 | 1,540 | 0.38 | - | 1.85 | 1,539 | 0.17 |
| Bm \times PC2 | - | 2.72 | 1,540 | 0.10 | - | 0.68 | 1,539 | 0.41 |
| Fm \times PC1 | 0.59 \pm 0.27 | 4.77 | 1,544 | 0.029 | - | 0.89 | 1,539 | 0.35 |
| Fm \times PC2 | - | 0.01 | 1,540 | 0.90 | - | 0.74 | 1,539 | 0.39 |
| Bm \times Fm \times sex | -0.72 \pm 0.28 | 6.55 | 1,544 | 0.011 | - | 1.21 | 1,534 | 0.27 |
| Bm \times PC1 \times sex | - | 0.50 | 1,536 | 0.48 | - | 0.16 | 1,534 | 0.69 |
| Bm \times PC2 \times sex | - | 0.51 | 1,536 | 0.47 | - | 0.29 | 1,534 | 0.59 |
| Fm \times PC1 \times sex | - | 0.01 | 1,536 | 0.93 | - | 0.02 | 1,534 | 0.90 |
| Fm \times PC2 \times sex | - | 0.70 | 1,536 | 0.40 | - | 1.17 | 1,534 | 0.28 |

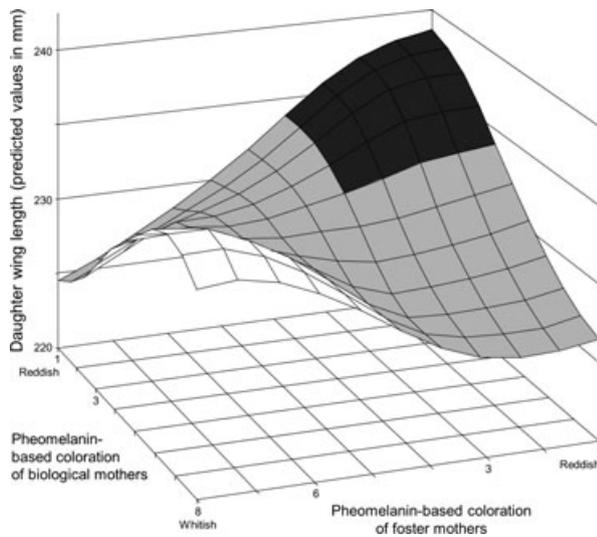


Fig. 6 Plumage-specific adaptations to rearing conditions. Wing length of fledgling female barn owls as a function of the pheomelanin-based coloration of both their biological and foster mothers. Surface plots are drawn from the predicted values of the final mixed model on the number of fledglings with bivariate spline method for the data set interpolation (Harder & Desmarais, 1972).

according to our findings (and see Frey *et al.*, 2011), no specific habitat provides a higher fitness to all individuals; therefore, no habitat should be globally preferred by all individuals. After the first reproduction, according to their phenotype, females seemed thus to settle preferentially in habitats where they produced more offspring and where nestling growth is favoured. Females would actively choose to settle in habitats where they have a higher expected fitness. In such optimal habitat, they produced more daughters than in suboptimal habitats, which is the sex that most benefits from habitat adequacy, in the light of our cross-fostering experiments. Based on these results, we could have expected pairing with respect to pheomelanin-based coloration to be assortative to produce daughters displaying coloration

adapted to the prevailing environment, which was not the case. However, assortative pairing would imply that females search for a mate displaying the same coloration as her in the habitat where she is locally adapted. Because with respect to coloration males are randomly distributed across habitats, pairing assortatively may be particularly costly potentially explaining why pairing was random. We cannot rule out that female choice of new site and habitat-specific reproductive success is due to something correlated to habitat in our population, for instance, a trait of male partners that we did not consider.

Female decision to disperse (depart from a breeding site) was not significantly linked to habitat. This may reveal that the fitness cost of dispersing is higher than the expected fitness benefit of finding more appropriate habitat. But once an individual has left a site, the choice of different options of settlement appears to rely partly on habitat characteristics. In yearlings, no correlation between colour phenotype and habitat was found. This is consistent with their lower competitiveness limiting their choice of breeding sites and excluding them from optimal habitats and could partly explain why yearlings have a poorer reproductive success than adults.

Ecological factors to which dark and pale pheomelanin individuals are potentially adapted

The evolutionary stability of colour morphs can be explained by various adaptations to local conditions (Hedrick, 1986; Skulason & Smith, 1995). For instance, colour morphs can be cryptic in alternative habitats (Hoekstra *et al.*, 2005) and thereby associated with foraging and anti-predator strategies (e.g. Jones *et al.*, 1977; Greco & Kevan, 1999). Melanin has also temperature-dependent effects (Sirikia *et al.*, 2010), and non-melanin forms show a higher reflectance and lower temperature excesses when irradiated than melanin forms (Berry & Willmer, 1986; Beasley & Ankney, 1988). This can explain why dark morphs can spend more time in shady habitats than pale morphs (Wunderle, 1981), a phenomenon that is particularly

Table 5 Synthesis of the main results of the present study carried out in the barn owl.

| Female breeder traits | Relationship with PC1 'Forest' | Relationship with PC2 'Field' |
|------------------------------------|---|-----------------------------------|
| Plumage whiteness | n.s. | – in old females |
| Site fidelity | n.s. | n.s. |
| Choice of new site | + in whitish/– in reddish females | n.s. |
| Assortative pairing | n.s. | n.s. |
| Hatching date | n.s. | n.s. |
| Number of fledglings produced | + in old whitish/– in old reddish females | n.s. |
| Proportion of daughters produced | n.s. | – in whitish/+ in reddish females |
| Size of fledglings produced | + in whitish/– in reddish females | n.s. |
| Body weight of fledglings produced | n.s. | n.s. |

The symbol '–' and '+' indicate the sign of correlations and 'n.s.' nonsignificant results. For instance, in individuals older than 2 years, females displaying a whiter plumage were located in habitats with more fields.

important in invertebrates (Ellers & Boggs, 2004) and ectothermes (Clusella Trullas *et al.*, 2007). Finally, morphs can be genetically correlated with other phenotypic traits that make them more or less susceptible to various sources of stress (Ducrest *et al.*, 2008; Karell *et al.*, 2011) inducing differently coloured individuals to exploit alternative habitats and to behave differently (review in Roulin, 2004b). For instance, a recent study in the rainbow trout (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*) showed that artificial selection for low and high hypothalamus–pituitary–interrenal responsiveness led to a change in melanin-based pigmentation. Darker eumelanic fish showed a reduced physiological and behavioural response to stress (Kittilsen *et al.*, 2009).

Here, we tested whether barn owls are locally adapted with respect to pheomelanin-based coloration and two eumelanin-based colour traits, namely number and size of black spots located at the tip of feathers. Our results showed no pattern of local adaptation with respect to number of eumelanic spots and spot size. This is consistent with the finding that within our study area, spot size is directionally selected in females indicating that large-spotted females achieve a higher fitness than small-spotted ones in any territory (Roulin *et al.*, 2010). With respect to pheomelanin-based coloration, we do not have yet identified the ecological factors that explain why whitish and reddish females performed the best in specific habitats in Switzerland and in different parts of the European continent (Antoniazza *et al.*, 2010). In our population, whitish females seemed to prefer and perform better in wooded area with fewer fields, whereas reddish females presented the opposite pattern. It is difficult to disentangle which habitat characteristic explains our results among field, forest area or altitude, because they are all highly correlated in the study area (Table 1). Correlative data suggest that pheomelanin-based coloration may play a role in predator–prey relationships, as in both allopatry and sympatry, whitish individuals predate more upon mice than reddish individuals that predate more upon voles (Roulin, 2004a). This finding is consistent with dark reddish females being located in sites surrounded by more arable fields and meadows, an habitat that is rich in common voles (*Microtus arvalis*) (Roulin, 2004a). In contrast to black spots, which occupy a small proportion of the plumage (between 0% and 15%), feathers of the ventral body side can be entirely white or dark reddish, having strong effect on the degree to which birds are cryptic when flying at night, at least for human eyes (A. Roulin, personal observation). Alternatively, habitat features could reflect the stress associated with human activities, more intense in arable fields for instance, and towards which reddish females would be more resistant than whitish ones.

The patterns of local adaptation reported in the present study may result from selection being exerted on coloration itself or from selection on genetically correlated traits (Ducrest *et al.*, 2008). Indirect selection has been

demonstrated in both the barn owl and the tawny owl (*Strix aluco*), as pheomelanin-based coloration covaries with physiological parameters associated with growth rate and immunity (Roulin, 2004d; Roulin *et al.*, 2008; Gasparini *et al.*, 2009; Piault *et al.*, 2009). The finding that daughters raised in foster nests grew longer wings if raised by foster mothers displaying a similar rather than dissimilar coloration as their biological mother is consistent with the hypothesis of indirect selection. Nestling physiology, reflected by their coloration, would fit some habitats better than others. Differential nestling growth would thus be due to an environmental factor that is correlated with female plumage coloration such as temperature, humidity or food resources.

Interestingly, the effect of habitat appears to be both sex- and age-specific because it was stronger in old females and not detected in males. Thus, it might be more important for some females to select the most appropriate habitats. To tackle this issue, we need to identify the ecological factors that are responsible for such effects and also to pinpoint which gene is sensitive to these factors in a sex-specific way.

Detecting adaptations at the continental vs. local scale

At large spatial scales, the environment varies in numerous ecological dimensions that likely constitute selective agents. Because important ecological parameters are expected to vary across continents, the action of selection at large spatial scales may be demonstrated in a straightforward way. However, the identification of the selective agents such as climatic and ecological variables, in turn, is tremendously difficult with problems of spatial autocorrelation, and hence approaches working at a more local scale are required.

At a smaller geographic scale such as in our study area of 190 km² the likelihood to detect patterns of local adaptation is much lower than at the continental scale, because environmental variation is probably less marked than at the extremity of the distributional range. In cavity-breeding species, competition for breeding sites is intense and hence individuals may also be relegated to territories where they are not locally adapted. Furthermore, as nest-boxes may not be placed in territories where environmental conditions are particularly suited to whitish and reddish individuals, it might be more difficult to find results consistent with the hypothesis of local adaptation than in a species in which individuals are free to choose their breeding site, an important condition that favours local adaptation and the maintenance of polymorphism (Ravigné *et al.*, 2004; Edelaar *et al.*, 2008).

Habitat characteristics of breeding sites were shown to explain a statistically significant but small proportion of the variance in breeding success and in the distribution of females among sites with respect to pheomelanin-based coloration. This effect was consistently found across

various life history traits in females (Table 5), strongly suggesting that it is reliable, albeit being small. This effect was less pronounced in 1-year-old females, which did not settle in sites according to their pheomelanin-based coloration and for which the number of fledglings did not vary in relation to habitat feature. Moreover, males did neither show colour-specific habitat selection nor colour-specific habitat effects on reproductive success. This raises the question of how such small-scale environmental variation contributes to the maintenance of polymorphism in this population located in the centre of the European cline variation. Colour-specific habitat selection of nonphilopatric females and habitat-dependent effects on female fitness may not be the force promoting diversification of phenotypes, but probably help maintaining phenotypic polymorphism.

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