

Breeding rate is associated with pheomelanism in male and with eumelanism in female barn owls

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Melanin-based coloration exists in 2 types: black eumelanism and reddish-brown pheomelanism, which both have a strong heritable component. To test whether these 2 types of melanism are associated with alternative adaptations, we carried out a correlative study over 8 years and an experiment in a Swiss population of barn owls, *Tyto alba*. This species varies in coloration from reddish-brown to white and from lightly to heavily marked with black spots. Based on the fact that plumage coloration and spottiness are male- and female-specific secondary sexual characters, respectively, we examined whether the probability of breeding is associated with the degree of pheomelanism in males and of eumelanism in females. In males, recruited nestlings were significantly less reddish-brown than their nonrecruited nest mates. In females, individuals displaying larger black spots started to breed at a younger age and had a higher survival, and females with experimentally reduced plumage spottiness bred less often than control females. Therefore, in the barn owl, the degree of male pheomelanism is associated with the probability of being recruited in the local population, whereas the degree of female eumelanism correlates with age at sexual maturity, survival probability, and also the probability of skipping reproduction. *Key words*: color polymorphism, female ornament, melanin, sexual maturity, survival, *Tyto alba*. [*Behav Ecol* 18:563–570 (2007)]

The maintenance of sexual dimorphism is a central issue in sexual selection theory. Sexual dimorphism can evolve and be maintained if selection on a trait differs between the sexes. The usual situation is where phenotypic selection favors males to be conspicuous (sexual selection) and females to be cryptic (natural selection). Less understood is the role of genetic correlations in promoting or constraining the evolution of secondary sexual characters. Empirical studies have suggested that selection exerted on one trait in one sex indirectly constrains the evolution of the same trait in the other sex (Price and Burley 1994; Chippindale et al. 2001; Fedorka and Mousseau 2004; Bonduriansky and Rowe 2005; Prasad et al. 2007). Another intricate possibility is where selection exerted on one trait in one sex affects the evolution of another trait in the other sex. This situation may take place if the 2 traits are genetically correlated both within individuals and between the sexes. Suitable model systems may be animals displaying melanin-based color traits because their expression is usually under strong genetic control (Bennett and Lamoreux 2003) and both males and females often display them (e.g., Roulin 2004a). A first step toward understanding the evolution of melanin-based color traits is to investigate sex-specific selection on these 2 traits.

Many animals vary in the degree of both black eumelanism and reddish-brown pheomelanism. This widespread interindividual variation has prompted intense work to find out its adaptive function (Majerus 1998; Hill 2006). Although doubts were raised about the possibility that the degree of melanism is sexually selected and could be associated with fitness com-

ponents (Badyaev and Hill 2000), accumulating evidence shows that melanism covaries with physiological, morphological, behavioral, and life-history traits and is a criterion in mate choice (reviews in Jawor and Breitwisch 2003; Roulin 2004a). However, there is still no consensus about the exact functional value of melanin-based coloration. The finding that the expression of melanism is under strong genetic control in many species and weakly sensitive to environmental factors (Hill and Brawner 1998, Roulin et al. 1998, Roulin and Dijkstra 2003 but see Griffith et al. 1999; Fargallo et al. forthcoming) suggests that melanin-based morphs achieve equal fitness under frequency-dependent or disruptive selection. Although in most cases animals vary continuously between extreme morphs, researchers usually categorize individuals in a discrete number of morphs with the idea that each morph is associated with alternative but equally rewarding strategies (e.g., reviews in Galeotti et al. 2003; Roulin 2004a; Dale 2006). Even though the degree of melanism can be correlated with some fitness components (e.g., melanic individuals are dominant in social interactions over nonmelanic ones, e.g., Breihagen and Saetre 1992), it may not be associated with absolute individual quality and in turn fitness. Therefore, in species in which interindividual variation in the degree of melanism is primarily under genetic control, melanin-based coloration may not be directionally selected but under frequency-dependent or disruptive selection.

Our goal in the present study is to investigate whether 2 melanin-based color traits in the barn owl are directionally selected or not in males and females. Barn owls vary in plumage coloration continuously from reddish-brown to white, a pheomelanin-based color trait, and continuously from lightly to heavily marked with black spots, a eumelanin-based trait. These 2 plumage traits are heritable and their expression is not sensitive to the environment and body condition, at least not to a detectable degree (Roulin et al. 1998; Roulin and

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Dijkstra 2003). Therefore, in the barn owl, both plumage coloration and plumage spottiness may not be directionally selected otherwise variation would be rapidly depleted. However, even if individuals of the 2 sexes can express any phenotype, males are on average whiter and less spotted than females (Roulin 2003). Because all birds become whiter between the first and second year of age (Roulin 1999a), sexual dimorphism in coloration may be maintained through selection favoring males to be white rather than females to be reddish-brown. Similarly, spot diameter increases in size between these 2 age classes in females only (Roulin A, unpublished data), and the size of black spots is positively correlated with fitness components in females (Roulin 2004b). This suggests that sexual dimorphism in plumage spottiness is maintained through selection exerted on females to be heavily spotted rather than on males to be lightly spotted. Therefore, it remains unclear whether plumage coloration and spottiness are directionally selected or not, and in which sex. This is particularly important because plumage coloration and spottiness are genetically correlated both within the sexes (spottier individuals are darker reddish-brown; Roulin 2004b) and between the sexes (darker and spottier parents produce offspring of the opposite sex that are darker and spottier; Roulin et al. 2001a). Therefore, directional selection exerted on plumage coloration in males might indirectly affect the evolution of plumage spottiness in females, whereas directional selection exerted on plumage spottiness in females might influence the evolution of plumage coloration in males.

To investigate predictions of the hypothesis that selection favors white over reddish-brown males and heavily over lightly spotted females, we examined whether the probability of being recruited as a breeder, age at sexual maturity, probability of skipping reproduction, and survival probability are associated with plumage coloration in males and with plumage spottiness in females. As a measure of recruitment probability, we compared plumage traits of nestlings that were recruited in the local breeding population with plumage traits of their nonrecruited same-sex nest mates. Plumage-dependent sexual maturity was assessed by comparing plumage traits of individuals that were recruited as breeder for the first time at the first year of age with individuals recruited at a later age. We could determine whether plumage spottiness causally determines the probability of renesting by manipulating the number of black spots displayed by breeding females. Finally, we applied capture–recapture models to investigate whether plumage traits are associated with survival.

METHODS

Study organism

The barn owl is nocturnal and preys mainly upon small mammals. The 2–13 eggs are laid between March and July, and eggs hatch asynchronously every 2.5 days creating a pronounced within-brood age hierarchy. Chicks gain body mass during the first 40 days of life, and then they lose weight until fledging occurring at 55 days. Females are heavier than males. Sexual maturity is usually reached within the first year of life but in some years birds can delay reproduction (Altwegg et al. 2007). All females breed by age 4 or 5, and all males breed by age 2 or 3 (Altwegg et al. 2007). A recent study on population dynamics showed that the probability of leaving the study area was 0.75 in juveniles and 0.01 in adults (Altwegg et al. 2003).

Assessment of plumage traits

The study was carried out in western Switzerland in an area covering 190 km². In 1987, we fixed 110 nest-boxes in barns

where most owls from our population breed. For each individual, coloration of the breast, belly, one flank, and underside of one wing was reliably compared with 8 color chips ranging from 1 for reddish-brown to 8 for white (Roulin 1999a). The mean value was our index of plumage coloration. On the same 4 body parts, we counted the number of spots in areas of 60 × 40 mm and measured to the nearest 0.1-mm spot diameters. Values found on the 2 flanks as well as those on the 2 wings were averaged, and then we calculated the mean value across the 4 body parts. The latter value was used in the statistical analyses. Assessment of number and size of black spots is reliable (Roulin 2004b).

Plumage-dependent recruitment as breeding birds

Between 1996 and 2003, we measured plumage traits of 1363 nestlings of known sex (for details about molecular analyses, see Roulin et al. 1999). From this sample of nestlings, we captured 52 males and 34 females breeding within our study area (i.e., recruits). Because they were not always raised alongside same-sex nest mates, we had a sample of 38 and 25 nests to compare coloration of recruited and nonrecruited male and female nest mates, respectively. In several years (1996, 1998, 2001, and 2002), we cross-fostered half the hatchlings between nests for other purposes than the one of the present study implying that recruited and nonrecruited nest mates were not always siblings. We therefore performed another test where we restricted the comparison between recruited and nonrecruited siblings raised in the same nest. When a nest produced more than one recruit (but also more than one nonrecruited nestling), we calculated the mean trait values to avoid pseudoreplication. In this way, each nest appears only once per analysis.

Plumage-specific age at first reproduction

Between 1996 and 2004, we monitored 502 nests where we captured and assessed plumage traits of 426 breeding males (84%) and 486 breeding females (97%). In total, we had a sample of 259 different breeding males and 304 different breeding females. Females were distinguished from males by the presence of a brood patch. Because we captured male and female breeders systematically from 1991 onward, we could determine whether birds captured between 1996 and 2004 started to breed in our study area as yearlings or adults (i.e., 2 years or older). Age in years was known accurately when birds had been ringed as nestlings. Otherwise, the birds were classified as “yearling” if their primary and secondary wing feathers belonged to the same new generation and “older” otherwise (Taylor 1993). This is important because males and females become slightly light colored between the first and second year of age (Roulin 1999a), and in females, spot diameter increases in size between these 2 age classes (Roulin A, unpublished data). However, a bird that was darker or spottier than another one in the first year of life was still darker or spottier in its second year (Roulin and Dijkstra 2003). Therefore, to assess whether age at first reproduction is a plumage-dependent life-history trait, we compared plumage traits measured after the first year in adults captured as breeders in their first year of life with adults captured for the first time as breeders at an older age. Because most birds breeding for the first time as 2 years old were not captured before, we considered only birds for which we measured plumage traits at the second year of age or after that age.

We tested experimentally whether plumage spottiness causally affects the probability of breeding in our study area. In 1997, when nestlings were on average 6 days of age, we cut off most spots located on the tip of the feathers of 16 females

(treatment “females with reduced plumage spottiness”), and for 17 other females, we cut off small pieces of the feathers but not the spots (treatment “females with spots”). As already shown elsewhere, females were randomly distributed into the 2 treatments with respect to clutch size, egg volume, hatching date, plumage coloration, and spottiness (Roulin 1999b). In 1999, we carried out a similar experiment with females being captured during incubation. Seventeen females were allocated in the treatment “females with reduced plumage spottiness” and 24 in the treatment “females with spots” (for more details, see Roulin et al. 2001b). Females from these 2 groups did not differ in age, coloration, number and size of spots, and in the size of their clutch, egg volume, and hatching date (Student's *t*-test: *P* values > 0.15). The aim of these experiments was to reduce female plumage spottiness not only in year *X* (i.e., 1997 and 1999) but also in year *X* + 1 (i.e., 1998 and 2000). We were successful because females with reduced plumage spottiness had fewer spots in year *X* + 1 compared with year *X* (on average they lost 4 spots), whereas females with spots had a similar amount of spots (on average they had one extra spot) (analysis of covariance [ANCOVA] with number of spots lost between year *X* and year *X* + 1 as dependent variable, treatment as a factor: $F_{1,34} = 5.28$, $P = 0.028$; number of spots in year *X* as a covariate: $F_{1,34} = 0.77$, $P = 0.39$).

Natal dispersal in relation to plumage traits

Results on plumage-dependent recruitment can be confounded by plumage-dependent emigration. To examine whether natal dispersal of juveniles in their first year of life is plumage dependent, we had a sample of 68 one-year-old male recruits and 63 female recruits captured between 1996 and 2004 for which natal site and plumage traits were assessed. Amateur ornithologists ringed 12 of these males and 35 of these females outside the study area. Distances between natal site and the site where yearlings bred for the first time were log transformed to normalize the data set. We performed an ANCOVA including year, region where recruits were born (i.e., within or outside the study area), sex, plumage coloration, number and size of spots, and interaction between sex and the 3 plumage traits.

Plumage-dependent survival: capture–recapture analysis

We carried out capture–recapture analyses to investigate whether survival was associated with plumage traits. We estimated survival and emigration using a combination of live-recapture and dead-recovery data. Between 1996 and 2003, we marked 1742 individuals (1363 of which were ringed as nestlings) of which 209 were later recaptured alive at least once (417 recaptures in total) and 120 were recovered dead. Accounting for the breeding phenology, we counted the years from March until February of the next year (February 2004 is the end point). Recently developed statistical methods account for the problem that not every breeding owl was captured in every year and allow the separation of true survival from emigration (Brownie et al. 1985; Lebreton et al. 1992; Burnham 1993). The statistical models consist of the following 4 components: the true survival rate (*S*), the recapture rate (*P*), which is the probability of capturing an individual at a particular occasion, given that it is alive and in the study area at that time, the recovery rate (*r*) describes the probability that a dead animal is recovered and reported, and the emigration rate (*E*), which is the probability for an individual of leaving the sampling area, given that it survived. Survival and emigration can be separated because dead owls are recovered from an unrestricted area (median and maximum

distances for recovered juvenile males: 11 and 758 km; juvenile females: 16.5 and 451 km; adult males: 4 and 19 km; and adult females: 16 and 571 km), whereas live birds can only be recaptured inside the study area. Therefore, if an individual leaves the study area, it is no longer at risk of being captured, but it can still be found and retrieved when it dies. In a previous study, we have used this modeling framework to examine the temporal patterns of survival and emigration for the same population of barn owls (Altwegg et al. 2003). Here, we extend the models to include the individual attributes of plumage coloration and spottiness and to estimate selection on these traits while accounting for the possibility that emigration is nonrandom with respect to the trait under consideration. In addition to our earlier study, we here also examine differences between the sexes and add 2 additional years of data.

Our most general model was informed by the results of our previous study (Altwegg et al. 2003) and contained the interactive effects of age, sex and year on survival and recovery rates, sex effects on recapture rates, and the interactive effects of age and sex on emigration rates (model 1, Table 1). This general model without individual covariates assumes that every marked individual in the population has the same probability of surviving, emigrating, and being recaptured or recovered at any occasion. We used separate goodness-of-fit (GOF) tests provided by the program RELEASE (Burnham et al. 1987) and the program ESTIMATE (Brownie et al. 1985) for the live-recapture and dead-recovery data, respectively. For both data types, the GOF test showed that models taking into account year and age effects fitted the data well (live recaptures: Tests 2 + 3, excluding Test 3.SR for birds ringed as nestlings, in program RELEASE: $\chi^2_{28} = 30.27$; dead recoveries: program ESTIMATE: $\chi^2_{14} = 21.83$, combined $P = 0.14$). An additional GOF test based on Monte Carlo simulations showed that overdispersion was low for our most general model (median *c*-hat approach, based on 20 simulations each at 12 levels of overdispersion: $\hat{c} = 1.14$, standard error = 0.02). Therefore, our data did not violate the assumptions of the modeling approach to a detectable degree, and the general model was a good starting point for model selection.

We analyzed survival and recapture rates in 2 steps. First, we sought the most parsimonious representation for all 4 model components with respect to the factors year, sex, and age. We considered 2 age classes, “juveniles” and “adults” (i.e., yearlings and older individuals). Then we examined survival and emigration of juveniles in relation to plumage traits while accounting for the effects found to be important in the first step of the analysis. All models were fitted using program MARK version 4.3 (White and Burnham 1999).

We followed basic model selection methodology (Lebreton et al. 1992; Burnham and Anderson 2002) and evaluated the fit of each model using Akaike's information criterion (AICc). The model with the lowest value of AICc is the most parsimonious one in the sense that it provides the best balance between overfitting (hence loss of precision) and underfitting (hence bias) and is the selected model. The Akaike weights give the relative support that a given model has from the data compared with the other models in the set (all information in Burnham and Anderson 2002).

Statistical procedure

Apart from capture–recapture analyses, statistical tests were computed with the JMP statistical package. We carried out nonparametric analyses when the data were not normally distributed. Statistical tests were 2-tailed and *P* values smaller than 0.05 considered significant. Means are quoted ± 1 SD.

Table 1
Effects of plumage characteristics on survival and emigration

	Survival	Recapture	Recovery	Emigration	<i>K</i>	Deviance	AICc	Delta AICc	Akaike weight
(A)									
(1)	Age × year × sex	Sex	Sex × age × year	Sex × age	65	362.695	2761.859	49.191	0.000
(2)	Age × year × sex	Constant	Age	Sex × age	39	394.530	2739.053	26.385	0.000
(3)	Age × year	Constant	Year	Sex × age	28	404.217	2726.027	13.359	0.001
(4)	Sex + age + year	Constant	Age + year	Sex + age	23	404.310	2715.873	3.205	0.147
(5)	Age + year	Constant	Age + year	Sex + age	22	406.763	2716.282	3.614	0.120
(6)	Age + year	Constant	Age	Sex + age	15	417.400	2712.668	0.000	0.732
(B)									
(6)	Age + year	Constant	Age	Sex + age	15	2682.443	2712.668	0.000	0.284
(7)	Age + year + color	Constant	Age	Sex + age	16	2680.630	2712.886	0.217	0.254
(8)	Age + year + sex + color	Constant	Age	Sex + age	17	2679.782	2714.069	1.401	0.141
(9)	Age + year + sex × color	Constant	Age	Sex + age	18	2678.791	2715.113	2.444	0.084
(10)	Age + year + color	Constant	Age	Sex + age + color	17	2680.013	2714.300	1.632	0.125
(11)	Age + year	Constant	Age	Sex + age + color	16	2682.271	2714.527	1.858	0.112
(C)									
(6)	Age + year	Constant	Age	Sex + age	15	2718.389	2748.614	9.806	0.007
(12)	Age + year + spots	Constant	Age	Sex + age	16	2718.064	2750.320	11.511	0.003
(13)	Age + year + sex + spots	Constant	Age	Sex + age	17	2712.140	2746.428	7.620	0.020
(14)	Age + year + sex × spots	Constant	Age	Sex + age	18	2702.486	2738.809	0.000	0.920
(15)	Age + year + spots	Constant	Age	Sex + age + spots	17	2712.635	2746.923	8.115	0.016
(16)	Age + year	Constant	Age	Sex + age + spots	16	2713.151	2745.407	6.599	0.034

The table shows a summary of the model selection for the analysis of combined ring-recovery and live-recapture data. The table shows the factors included in the survival, recapture, recovery, and emigration components of the model. Interactions between 2 variables are denoted by “×,” whereas purely additive models are denoted by “+.” When we included interactions, we always retained the corresponding main effects as well. The analysis proceeded in 3 steps, and we used logit-link functions throughout: (A) we first simplified our general starting model (model 1, for which we tested GOF) until we arrived at the simplest acceptable model without individual covariates (model 6). (B) In a second step, we examined versions of this model including the covariate plumage coloration (models 7–11). (C) Finally, we included the covariate spot diameter. Model selection was based on AICc, and delta AICc is the difference between a particular model and the best one within each subanalysis (in bold). Note that model 6 is included in all subanalyses as a reference model without covariates. Its AICc slightly varies because we lacked measurements of spot diameter for 6 individuals. Because the data changed, these AICc values are not comparable between models in (C) and models in the rest of the table. *K* is the number of estimated parameters. Deviance is the difference in log likelihood between the current and the saturated model, the latter being a model with number of parameters equal to the sample size. Deviances given here differ from $-2 \log$ (likelihood) by a constant, and differences in deviance can therefore be used to construct likelihood ratio tests between nested models. Akaike weights show the relative support a given model has from the data compared with the other models in the set.

RESULTS

Recruitment is associated with pheomelanism in males

The difference in plumage coloration between recruited and nonrecruited nest mates is sex specific (repeated measures analysis of variance [ANOVA], coloration of recruited and nonrecruited male and female nest mates as repeats, interaction between repeats and sex: $F_{1,61} = 9.18$, $P = 0.0036$). Recruited male nestlings were significantly lighter colored than their nonrecruited male nest mates (paired *t*-test: $t_{37} = 3.15$, $P = 0.0032$; means are 6.01 vs. 5.38; Figure 1a), whereas recruited females were nonsignificantly darker colored than their nonrecruited female nest mates ($t_{24} = 1.33$, $P = 0.19$; means are 4.45 vs. 4.77; Figure 1b). Applying similar repeated measures ANOVA, recruited and nonrecruited nest mates did not differ in number of spots and spot diameter (all *P* values > 0.35; interaction between repeated measures and sex, all *P* values > 0.18). If we restrict the analysis to siblings raised in the same nest, mean plumage coloration of recruited and nonrecruited males was not significantly different ($t_{26} = 1.91$, $P = 0.067$). This nonsignificant result may be due to a lack of power because plumage coloration measured on the belly of recruited males was significantly lighter than that of their nonrecruited same-sex siblings

raised in the same nest ($t_{26} = 2.54$, $P = 0.018$; means are 6.80 vs. 6.18).

Age at sexual maturity is associated with eumelanism in females

In a stepwise logistic regression (Table 2), the likelihood that an individual is captured for the first time as a breeder at the first year of age was associated with year, sex (66.7% and 52% of males and females breed for the first time as yearlings, respectively) and spot diameter with spottier individuals breeding for the first time at a younger age, an effect that was significantly stronger in females (Student's *t*-test: $t_{148} = 3.44$, $P = 0.0008$) than in males ($t_{124} = 1.63$, $P = 0.11$) (Table 2 and Figure 2a). There was a significant interaction between plumage coloration and sex on the age at maturity (Table 2 and Figure 2b) with darker males tending to breed at a younger age ($t_{124} = 1.49$, $P = 0.14$), whereas the opposite trend was detected in females ($t_{148} = -1.67$, $P = 0.10$). To examine whether the relationship between spot diameter and age at maturity was confounded by the origin of the birds, we considered only individuals ringed as nestlings because we know whether they were born within ($n = 82$ residents) or outside the study area ($n = 42$ immigrants). Again, individuals breeding for the first time as yearlings had larger spots than individuals

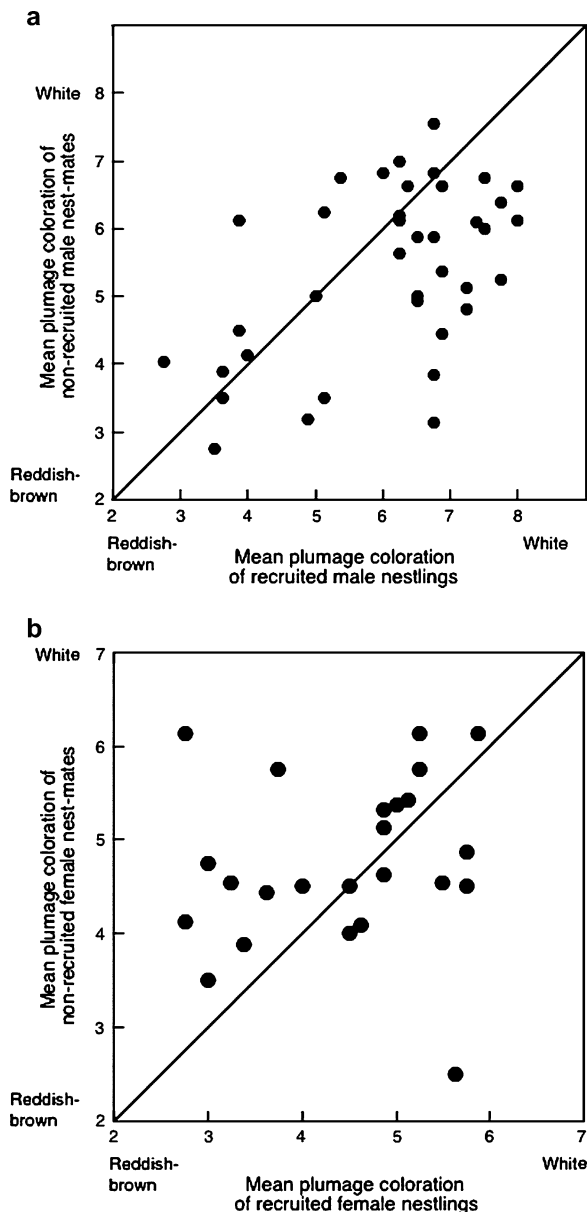


Figure 1
 Mean plumage coloration of recruited and nonrecruited male (a) and female (b) nest mates. Data points on the diagonal represent recruited and nonrecruited nest mates that were equally colored.

breeding for the first time at a later age (similar stepwise logistic regression as in Table 2—spot diameter: Wald $\chi^2_1 = 6.19$, $P = 0.013$; immigrant vs. resident: $\chi^2_1 = 6.17$, $P = 0.013$, resident individuals started to breed in the study area at a younger age than immigrants). In a model with spot diameter as the dependent variable, the interaction between sex and region where recruits were born was on the borderline of significance (2-way ANOVA—sex: $F_{1,119} = 37.52$, $P < 0.0001$; age at first reproduction: $F_{1,119} = 8.90$, $P = 0.0035$; immigrant vs. resident: $F_{1,119} = 0.36$, $P = 0.54$; interaction sex by immigrant vs. resident: $F_{1,119} = 3.70$, $P = 0.05$). Resident females displayed larger spots than immigrant females (Student's t -test: $t_{50} = 3.14$, $P = 0.0028$; Figure 3), whereas this difference was not significant in males ($t_{70} = 0.40$, $P = 0.69$; Figure 3). Similar analyses on plumage coloration and number of spots were not significant.

Table 2

Stepwise logistic regression on the age (yearling vs. adult) at which the individuals were captured for the first time as a breeder in relation to year (1993–2004), sex, plumage coloration, number of spots, and spot diameter

Source of variation	df	Wald χ^2	P
Year	11	28.97	0.0023
Sex	1	14.40	0.0001
Color	1	0.10	0.75
Spot diameter	1	10.21	0.0014
Color \times sex	1	4.91	0.027
Spot diameter \times sex	1	3.70	0.05
Rejected terms			
Number of spots \times sex	1	0.15	0.69
Number of spots	1	0.71	0.40

Interactions between 2 variables are denoted by “ \times ”; df: degrees of freedom.

Probability of renesting is associated with eumelanism in females

The effect of the manipulation of plumage spottiness on the probability of renesting differed between years (logistic regression with the probability of renesting [0/1] as the dependent variable—manipulation of plumage spottiness: Wald $\chi^2_1 = 0.80$, $P = 0.37$; year (1997 vs. 1999): Wald $\chi^2_1 = 0.06$, $P = 0.80$; age in years: Wald $\chi^2_1 = 3.54$, $P = 0.06$; interaction year by manipulation of plumage spottiness: Wald $\chi^2_1 = 3.59$, $P = 0.05$). In 1997, females for which we cut off black spots did not breed more often the following year (9 out of 16 individuals, 56%) than those for which we did not cut off black spots (8 out of 17 individuals, 47%, chi-square test: $\chi^2_1 = 0.28$, $P = 0.60$). In 1999, females for which we cut off spots were less likely to breed in the following year (5 out of 17 individuals, 29%) than females for which we did not cut off black spots (15 out of 24 individuals, 63%; $\chi^2_1 = 4.46$, $P = 0.03$).

Natal dispersal is not related to plumage traits

Male and female recruits moved on average 12 ± 15 km (median is 6 km) and 23 ± 21 km (median is 16) between the natal nest and the site where they bred in their first year of life, respectively. After controlling for year and the region where recruits were ringed (i.e., within or outside the study area), natal dispersal was not associated with plumage coloration, number of spots, and spot diameter (ANCOVA: all P values > 0.10 ; all interactions between sex and plumage traits were not significant and hence removed from the model).

Survival probability is associated with eumelanism in females

The most parsimonious model excluding plumage characteristics accounted for differences between juveniles and adults in survival, emigration, and recovery rate of dead owls (model 6 in Table 1A). Furthermore, survival varied over the years, and recapture rates of live owls was constant over the study period, thus confirming our earlier results for the same population (Altwegg et al. 2003).

Including plumage coloration did not improve the models, even though model 7, representing an effect of coloration on survival, was nearly as well supported as model 6 without coloration (Table 1B). The survival rate tended to increase by a factor 1.23 (95% confidence interval [CI] = 0.99–1.69; because the CI overlaps 1, this effect is not statistically significant) per score with whiter plumage. There was no evidence

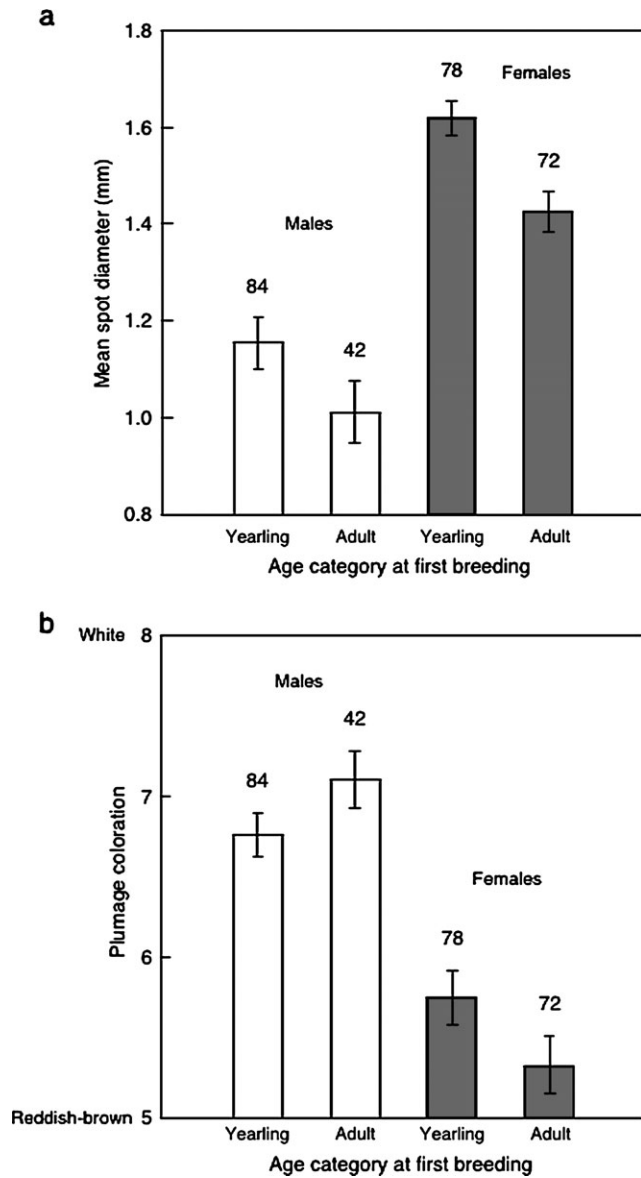


Figure 2 Mean spot diameter (\pm SE) (a) and coloration (b) in males and females breeding for the first time in their first year of age (yearling) and after that age (adult). Numbers above bars indicate sample size.

for sex-specific relationship between coloration and the survival rate (models 8 and 9) or for a relationship between coloration and emigration (models 10 and 11).

Including spot diameter improved the models and the best model included interactive effects of sex and spot diameter on survival (model 14, Table 1C, likelihood ratio test $\chi^2_3 = 15.9$, $P = 0.001$). Female survival increased with increasing spot diameter (by a factor 1.11 [95%CI = 1.043–1.18] per 0.1 mm), whereas male survival was not significantly related to spot diameter (0.977 [95%CI = 0.928–1.030], the CI overlaps 1) (Figure 4).

Spot diameter increases in size in females between the first and second year of age (Roulin A, unpublished data), and color changes in males and females at the same age (Roulin 1999a). Therefore, we reran the analysis restricting the capture–recapture model to individuals less than 2 years of age. This analysis did not change qualitatively.

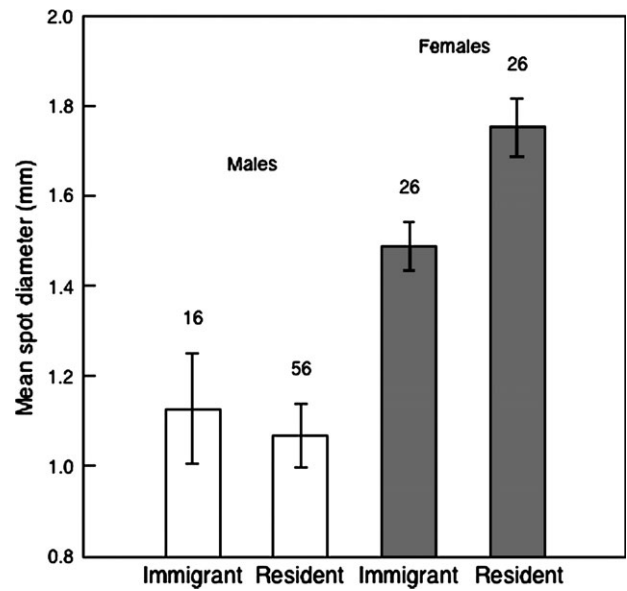


Figure 3 Mean spot diameter (\pm SE) in male and female immigrants and residents. All individuals have been measured at the second year of age or later. Numbers above bars indicate sample size.

DISCUSSION

The barn owl displays 2 melanin-based color traits that are genetically correlated within individuals (darker reddish-brown birds being heavily spotted) and between the sexes (Roulin et al. 2001a; Roulin 2004b). Selection exerted on one trait in one sex may therefore indirectly influence the evolutionary trajectory of the other trait in the other sex. Investigating this scenario requires a detailed knowledge of the quantitative genetics of melanin-based coloration and of how selection is exerted on these color traits in the 2 sexes. In the present paper, we examined the latter point.

Recruitment is associated with pheomelanism in males

The present study shows that white male fledglings were recruited more often than their reddish-brown nest mates. The method of comparing coloration in recruited and non-recruited nestlings raised in the same nest is powerful because they experienced similar environmental conditions during

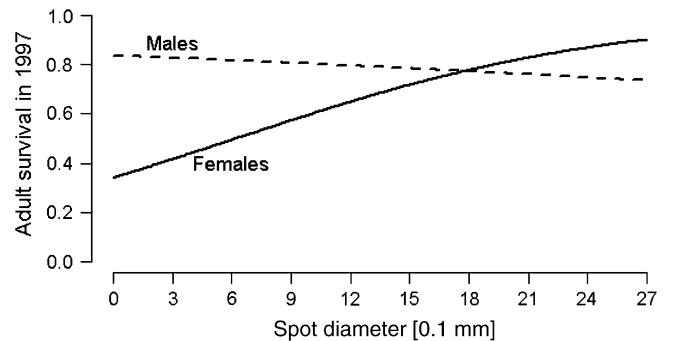


Figure 4 Relationship between survival and plumage spot diameter. As an example, we considered survival between 1996 and 1997 (the relationship was the same in all years, but mean survival differed among years). The straight line is for females and the dashed line for males.

the nestling stage and became independent from their parents at the same place and time. As a consequence, they had similar opportunities to find a nest site and mate for their first breeding attempt. This result was not confounded by color-specific nestling body condition (Roulin 2006), dispersal, and age at maturity. Survival and emigration probabilities were not associated with plumage coloration in our population. We are aware of only one previous study testing whether the degree of melanism is associated with age at maturity. In the Arctic skua (*Stercorarius parasiticus*), eumelanic individuals start to breed at about 4.5 years old, whereas non-eumelanic birds at 4 years old on average (O'Donald 1983).

Lighter colored male barn owls were more often recruited in the breeding population because they had an advantage under sexual or natural selection. Direct evidence that females mate preferentially with white males or that white males dominate reddish-brown males in intrasexual selection is still unavailable. We therefore discuss the alternative that white males had an advantage under natural selection. This alternative scenario is unlikely for the following 4 reasons. First, a previous study in the same area showed that reddish-brown males foraged more frequently for their brood and thereby produced more offspring than white males in 1997 (Roulin et al. 2001a) but also in 1994 (Roulin A, unpublished data). Given that reddish-brown and white birds have a different diet (Roulin 2004c), this observation suggests that in our study area foraging conditions are sometimes better for reddish-brown males. Second, if environmental conditions prevailing in our study area were not appropriate to reddish-brown birds, they should have emigrated out of the study area more often than white males or their survival should have been lower. This was not the case. Third, if natural selection was favoring white individuals in our study area, white females may have been recruited more often than their reddish-brown female nest mates. In contrast, and as can be seen in Figure 1b, females that were recruited tended to be more reddish-brown than their nonrecruited female nest mates. Fourth, because survival prospects are significantly lower in yearlings compared with older barn owls (Altwegg et al. 2007), a white coloration should be more beneficial in yearlings than in adults. However, between the first year and second year of life, males and females become lighter colored (Roulin 1999a). These 4 arguments may be taken as preliminary indications that inter- or intrasexual selection plays some role in the maintenance of sexual dimorphism in plumage coloration in the barn owl.

Age at maturity, probability of renesting, and survival are associated with eumelanism in females

Correlative data showed that females displaying larger black spots bred at an earlier age, and experimental data showed that plumage spottiness may causally affect the probability of breeding in females. The latter result was detected in females manipulated in 1999 but not in 1997 perhaps because the benefit of being heavily spotted varies between years. To our knowledge, this is the first experiment showing that manipulation of a female ornament affects the probability of renesting (see Cuervo et al. 2003). A link between the degree of melanism and survival was reported in the feral pigeon (*Columba livia*) (Johnston and Janiga 1995), the tawny owl (*Strix aluco*) (Galeotti and Cesaris 1996; but see Roulin et al. 2003), and in the lesser snow goose (*Anser caerulescens caerulescens*) (Cooch 1961; Cooke et al. 1995; but see Rockwell et al. 1985) but not in the Arctic skua (O'Donald 1983; Phillips and Furness 1998) and house sparrow (Jensen et al. 2004).

As for males, we discuss whether plumage spottiness is sexually selected. Apart from the fact that plumage spottiness of the mother is not associated with offspring body size (Roulin

2006), we do not possess any data to discuss whether heavily spotted females are dominant in social relationships, for instance, to secure a male and nest site. For this reason, we cannot discuss further a potential role of female plumage spottiness in intrasexual selection. The scenario of intersexual selection is consistent with a previous study showing that males do not pair randomly with respect to female plumage spottiness and also invest more effort in feeding rate when mated with spottier females (Roulin 1999b), probably because the size of black spots in females covaries positively with offspring humoral immunocompetence, parasite resistance, developmental homeostasis (Roulin 2004b), calcium physiology (Roulin et al. 2006), and the probability of surviving from one year to the next (present study). This suggests that female plumage spottiness is an ornament that males assess to choose a partner because this trait may reflect overall genetic quality.

Implications on the maintenance of genetic variation in melanism

Interindividual variation in the size of black spots has a strong genetic basis and is not sensitive to the rearing environment (Roulin et al. 1998; Roulin and Dijkstra 2003). To date, we found only evidences for a beneficial role of displaying large black spots (Roulin 2004b; Roulin et al. 2006; present study), suggesting that females are directionally selected to display large spots. Therefore, the maintenance of variation in plumage spottiness in the face of directional selection remains an enigma. A possibility is a high mutation rate in the size of black spots that would replenish genetic variation. No data are available on this issue. A second possibility is gene flow of lightly spotted individuals from surrounding populations (e.g., Lawson 1996; Merilaita 2001). This is possible because in females, but not in males, immigrants displayed smaller black spots than residents. This scenario can apply to our population, but it cannot explain how sexual dimorphism in plumage spottiness is maintained everywhere in the world with females being on average more heavily spotted than males (Roulin 2003). A third possibility is that large black spots are counterselected in males in a way that positive selection in females and negative selection in males counterbalance each other (Houtman and Falls 1994; Price and Burley 1994). This scenario is possible because plumage spottiness is genetically correlated within and between the sexes (Roulin et al. 2001a; Roulin 2004b). Fourth, females displaying large black spots derive benefits with respect to a number of fitness components but may be penalized with respect to some other components that have not yet been determined (Hunt et al. 2004).

In conclusion, our results suggest that 2 aspects of barn owl plumage, pheomelanistic coloration and eumelanistic spottiness, are under different selective pressures in the 2 sexes. The next step is to examine the genetic correlations between the traits and the sexes in order to find out in what way selection on one sex affects or constrains the evolution of plumage in the other sex.

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