

Female colour polymorphism covaries with reproductive strategies in the tawny owl *Strix aluco*

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Roulin, A., Ducret, B., Ravussin, P.-A. and Altwegg, R. 2003. Female colour polymorphism covaries with reproductive strategies in the tawny owl *Strix aluco*. – J. Avian Biol. 34: 393–401.

Variation in coloration with a strong underlying genetic basis is frequently found in birds, insects, anurans, molluscs and plants. Although such a variation can be large, little is known about its functional value. Correlative data, however, can help suggest testable hypotheses about potential covariation between reproductive parameters and a colour polymorphism displayed by individuals belonging to a single population. In this context, we studied two Swiss populations of tawny owls *Strix aluco*, a polymorphic species that varies in coloration from reddish-brown to grey. Observations in the first population showed that although greyer females had shorter tarsi, they produced heavier offspring in two of three years. Pairing with respect to plumage coloration was not significantly disassortative, indicating that these correlations were probably not inflated by plumage coloration of the mate. In the second population, where breeding females had been monitored for 14 years, the proportion of all breeding females that were reddish-brown was greater in years when the breeding density was lower. Capture-recapture analyses show that the latter result is explained by the fact that greyish females bred less often than reddish-brown females, although their survival probability was similar. The number of greyer breeding females was greater when spring/summer temperatures were lower. When combined, the results from the two populations lend support to the hypothesis that grey females do not breed every year, but produce offspring of higher quality. Whatever the mechanism underlying the correlations reported in this study, colour polymorphism in female tawny owls appears to reflect some components of individual quality.

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Genetically-based variation in plumage coloration is a common feature in many groups of birds including seabirds, herons, raptors and owls (Huxley 1955, Salamonsen 1970, Paulson 1973, Lank et al. 1995, Roulin et al. 1998, König et al. 1999, Roulin and Dijkstra 2003). In polymorphic species, individuals that belong to the same population can display various colour variants. For example, in the eastern screech owl *Otus asio*, males and females belonging to all age classes can have a red, grey or intermediate plumage, with the expression of each coloration being inherited from one generation to the next (Hasbrouck 1893, Hrubant 1955), and in the barn owl *Tyto alba* variation from reddish-brown

to white is under genetic control but not sensitive to the environment and body condition (Roulin et al. 1998, Roulin and Dijkstra 2003). Although colour polymorphism occurs across a wide range of bird species and has interested evolutionary biologists for many years (Huxley 1955, Mather 1955), it is still far from certain whether different colorations reflect alternative foraging, reproductive or anti-predator strategies of a similar fitness value and this is exemplified by the absence of any relationship between colour morphs and reproductive parameters in a long-term study of the snow goose *Anser caerulescens caerulescens* (Cooke et al. 1995). However, the observations that differently coloured

individuals behave differently (Arnason 1978, Ficken et al. 1978, Nuechterlein 1981), adopt different mating (Hogan-Warburg 1966) or reproductive strategies (Furness 1987, Johnston and Janiga 1995, Roulin et al. 2001a), live in different habitats (Craig 1972, Birkhead et al. 1980, Wunderle 1981, Knapton and Falls 1982, Saino 1992), or differ in size (Rising and Shields 1980, Höglund and Lundberg 1989) or their physiological attributes (Mosher and Henny 1976, Roulin et al. 2000, 2001a, b) suggest that in many species, plumage polymorphism is not selectively neutral with respect to life history components. Individuals displaying a different coloration may achieve the same fitness via different routes, enabling the polymorphism to be maintained.

Assuming that colour variants that are genetically inherited and not sensitive to environmental variation reflect different ways or strategies of coping with a variety of ecological factors (e.g. food availability or weather conditions, Mosher and Henny 1976, Wunderle 1981), or resolving trade-offs between competing life-history components (e.g. reproductive effort vs. longevity), could reflect that morph-dependent reproductive success may vary between years. For instance, if individuals of a given coloration are adapted to cold, dry climates and individuals of another coloration to warm, wet climates, as it may be the case in the tawny owl *Strix aluco* (Galeotti and Cesaris 1996), the annual breeding success of the two different categories of birds may fluctuate and one coloration may have higher or lower success depending on the weather conditions. This example emphasises the need to search for correlates of plumage polymorphism by performing detailed short-term studies combined with the long-term monitoring of natural populations. Long-term studies are not only necessary to record annual variation in reproductive success that could be linked to coloration, but also to determine colour-dependent survival probabilities. Such correlative studies are important to generate testable predictions about what could be the signalling function of genetic colour polymorphism.

In the present study, we examine whether plumage coloration correlates with reproductive strategies in the tawny owl. We used data from a short-term and a long-term study of two Swiss study areas to investigate whether (1) pairing with respect to coloration is assortative, disassortative or random, (2) plumage coloration covaries with body size and altitude, (3) the proportion of breeding individuals that display a given coloration correlates with ambient temperature, and (4) plumage coloration correlates with reproductive success, and the probability of surviving and skipping reproduction. It is of importance to determine whether pairing is (dis)assortative because in this case any relationship between female plumage coloration and re-

productive success may in fact be confounded by plumage coloration of the mate.

Methods

The tawny owl

The tawny owl is one of the most common owl species in Central Europe. It is monogamous, philopatric, can live for more than 20 years and in some years some individuals do not breed. Body mass varies between 335 and 780 g, with females being larger than males (Baudvin and Dessolin 1992). It preys upon a variety of mammals, birds, frogs and reptiles, and is mainly found in forests where it breeds in tree holes or in the abandoned nests of raptors and crows (Cramp and Simmons 1985, Roulin and Ducret 1997). Hatching occurs early in the year (March to May) and brood size varies from one to seven. Though birds can be classified into three or more categories of coloration, plumage varies continuously from reddish-brown to grey. This variation is not sex-limited with individuals of one sex being as likely to display a given coloration as an individual of the other sex (Baudvin and Dessolin 1992, Galeotti and Cesaris 1996).

Long-term study

From 1987 to 2000, P.-A. Ravussin and colleagues studied a population in western Switzerland. In a woodland area covering 600 km², located at an altitude of 420 to 920 m, 112 nest-boxes were hung to trees. Each year we visited all boxes, and 464 breeding females (86% of 539 individuals) and 13 different breeding males were captured. Based on the extent to which each bird displayed reddish-brown feathers, they were classified into the categories 'Red', 'Red-Grey' and 'Grey'. In 2002, we tested whether the method of assessing plumage coloration is reliable. P.-A. Ravussin classified 35 adults into the same three colour categories and A. Roulin collected one feather on their back. These feathers were later ranked from the most red (rank 1) to the most grey ones (rank 35). Mean rank of 15 'Red' birds was 9.2, of seven 'Red-Grey' individuals 17.1 and of 13 'Grey' ones 28.6 (ANOVA: $F_{2,32} = 44.87$, $P < 0.001$) demonstrating that the method of classifying birds into three classes of colours is reliable. Assuming that females do not change in coloration from one year to the next, some of them (41 out of 148) were nevertheless classified into a different colour type in different years, suggesting that the use of discrete colour scores is not perfect. Note that among females classified into a different coloration, an approximately similar number of individuals were classified as redder ($n = 22$) or greyer

($n = 19$; sign test: $P = 0.76$). At the time of ringing, when they were 13–35 days old, P.-A. Ravussin or his colleagues weighed nestlings to the nearest g and measured one of their wings to the nearest mm. Wing length is a good indicator of age (Melde 1984). Ambient winter (December to March) and spring/summer (May to September) temperatures were measured from 1987 to 2000 in Bern about 80 km from the study area.

Short-term study

In order to obtain detailed data on the variation in plumage coloration, we studied another Swiss population located in the Broye plain at an altitude between 430 and 750 m. The two study areas are separated by a distance of 40 km. Over an area of 500 km², 87 nest-boxes, hung to tree trunks, had been present since 1986. From 1997 to 1999 we checked these boxes to capture breeding females for which a single person (A. Roulin) measured body mass, wing length and tail length. Tarsus length was measured only in 1998 and 1999. When nestlings were old enough to be ringed, B. Ducret took measurements of body mass and wing length. In each year, residuals from the regression of mean nestling body mass on mean nestling wing length provided an index of nestling body condition.

To assess plumage coloration precisely, A. Roulin collected a single feather from each individual from each of the following areas: breast, flank, back, lesser-covert, scapular and undertail-covert. On each individual, two feathers of the same body part are uniform in coloration and the collected feather was randomly selected. For each type of feather, A. Roulin ranked all females breeding from 1997 to 1999 from the most reddish-brown (rank 1) to the most grey (rank 51). A mean rank was calculated from all six feathers and this value was used in statistical analyses (simply referred to as 'female plumage coloration'). In 2001, ranks were assigned blind as to the identity of the females to which the feathers belonged. Mean rank in plumage coloration for a female in one year was similar to that measured in another year (repeatability analysis, $r = 0.91 \pm 0.03$ (SE), $F_{20,28} = 21.5$, $P < 0.001$) and variation in plumage coloration is therefore much greater between than within individuals, thus demonstrating the accuracy of our scoring system.

To examine whether owls do not pair randomly with respect to plumage coloration, we collected feathers of two breeding pairs captured in 1997 and five pairs in 1999. To increase sample size, we also considered three pairs captured in 2001 and four pairs in 2002. Using the same method as the one described above, we ranked these 14 females from the most reddish-brown to the most grey. We applied the same procedure to rank the 14 breeding males.

Survival analysis

We used capture-mark-recapture (CMR) methods to calculate annual survival rate, and thus accounted for the problem that not every owl was captured in every year (Lebreton et al. 1992, Nichols 1992). These methods allowed us to model the recapture rate, which is the probability of capturing an individual, given that it is alive, independently of the survival rate. Survival estimates are unbiased under the assumption that every marked individual in the population has the same probability of surviving and of being recaptured at any occasion. We tested these assumptions using the Goodness-Of-Fit (GOF) test provided by the program RELEASE (Burnham et al. 1987). The GOF test for the model assuming time dependent survival and recapture rates was not significant (Test 2 + 3:2 = 35.4, $df = 33$, $P = 0.36$), and our data thus met the assumptions of the modelling approach.

We investigated variation in survival and recapture rates between the years, and differences in survival between colour types. Furthermore, we considered models assuming that survival varied in relation to breeding population density. A model including the interaction between colour type and population density represented the hypothesis that one colour type survives better under high density whereas the other one fares better at low densities. We followed basic model selection methodology (Lebreton et al. 1992, Burnham and Anderson 1998) and evaluated the fit of each model using Akaike's Information Criterion (AICc). The model with the lowest value of AICc provides the best balance between overfitting (hence loss of precision) and underfitting (hence bias) and is the selected model (Burnham and Anderson 1998). Models within two AICc units of the best model are considered competitive. A difference of two to seven units indicates considerably worse fit of the model with the higher AICc value. A model with a difference of more than seven units provides a bad fit to the data (Burnham and Anderson 1998). The Akaike weights give the relative support that a given model has compared to the other models in the set (Burnham and Anderson 1998, p. 123).

Statistics

To examine whether female plumage coloration correlates with altitude in the short-term study, wing length, tail length and tarsus length, we pooled data collected from 1997 to 1999. Data from females captured in several years were averaged so that an individual appeared only once in each analysis. Data followed a normal distribution except for hatching dates in 1999 and to normalise these data, we transformed hatching dates with a \log_{10} function. For the statistical analyses,

Table 1. Number of breeding pairs, Grey, Red–Grey and Red breeding females, mean brood size (per successful and attempted nest), mean hatching date, nestling body condition, winter and spring/summer temperatures (T) for the long-term study. Mean nestling body condition was calculated from the second-order curve of logBody mass on logWing length (data from all years pooled).

Year	Grey females	Red–Grey females	Red females	Breeding pairs	Fledglings/successful nest	Fledglings/attempted nest	Hatching date	Body condition	Spring/summer T	Mean winter T
1987	5	0	8	24	3.38	2.96	3 Apr	0.029	15.06	1.96
1988	10	2	11	37	3.28	2.84	6 Apr	−0.001	15.71	1.53
1989	12	2	15	36	2.41	1.51	12 Apr	−0.024	15.83	2.05
1990	15	6	23	49	3.72	3.33	28 March	0.004	15.96	−0.58
1991	14	10	20	53	2.95	2.06	7 Apr	0.004	15.86	−0.82
1992	6	6	9	26	2.15	1.08	25 Apr	−0.008	16.54	0.69
1993	19	15	27	67	4.29	3.58	17 March	−0.004	15.70	2.67
1994	0	4	7	12	1.80	0.82	10 Apr	0.022	16.85	2.36
1995	15	14	20	61	3.48	2.88	31 March	−0.007	15.54	−0.16
1996	13	10	22	49	3.78	2.89	3 Apr	0	14.84	0.85
1997	2	4	8	14	2.75	1.57	1 Apr	0.014	16.22	2.31
1998	6	10	23	44	2.42	2.42	9 Apr	0.01	16.76	0.14
1999	5	6	18	30	3.08	2.55	15 March	−0.031	17.08	1.73
2000	5	9	18	42	4.28	4.28	24 March	0.005	16.68	2.74

Table 2. Number of breeding pairs, mean brood size, hatching date and nestling body condition for the short-term study. Mean nestling body condition was calculated from the regression of logBody mass on logWing length (data from all years pooled: $\log\text{Mass} = 1.416 + 0.508 \times \log\text{Wing}$).

Year	Number of breeding pairs	Number of fledglings per successful nest	Number of fledglings per attempted nest	Mean hatching date	Nestling body condition
1997	17	2.80	2.47	25 March	−0.019
1998	31	2.59	2.26	31 March	−0.003
1999	33	3.55	3.12	31 March	0.012

we used the package JMP (Sall and Lehman 1996). All tests were two-tailed and P-values smaller than 0.05 are considered significant. Means are given with ± 1 SD unless stated otherwise.

Results

Annual variation in breeding parameters

Number of breeding pairs, mean brood size, hatching date, nestling body condition and ambient temperatures are given in Table 1 (long-term study) and Table 2 (short-term study). Over the years and the two study areas mean hatching date was the first of April, and successful nests produced on average 3.1 fledglings.

Pairing with respect to plumage coloration

Data from the long-term study is consistent with the hypothesis that mating is random with respect to plumage coloration, since in nest-boxes where both partners were captured they did not necessarily have the same or different plumage coloration (Table 3). In the short-term study, pairing with respect to plumage

coloration was not significantly disassortative (Pearson correlation between colour ranks of female and male partners: $r = -0.34$, $n = 15$, $P = 0.23$). We can nevertheless not accept the null hypothesis that mating is random because sample sizes were too small.

Plumage coloration, body size and altitude

Long-term study

Red, Red–Grey and Grey females did not differ significantly in wing length (ANOVA: $F_{2,202} = 0.16$, $P = 0.85$) or body mass ($F_{2,187} = 0.70$, $P = 0.50$). They also bred at a similar altitude ($F_{2,194} = 0.23$, $P = 0.80$).

Table 3. Number of matings between different colour type combinations. Data are from the long-term study (13 different breeding pairs).

	Female coloration		
	Red	Red–Grey	Grey
Male coloration			
Red	2	2	1
Red–Grey	1	2	2
Grey	2	0	1

Short-term study

Female plumage coloration was not significantly correlated with altitude ($r = -0.03$, $n = 51$, $P = 0.85$), body mass ($r = -0.04$, $n = 50$, $P = 0.80$), tail length ($r = 0.13$, $n = 51$, $P = 0.35$), or wing length ($r = 0.20$, $n = 51$, $P = 0.16$). However, we found a negative correlation between female plumage coloration and tarsus length ($r = -0.43$, $n = 47$, $P = 0.003$; still significant after sequential Bonferroni correction for multiple tests, Fig. 1), indicating that greyer breeding females had shorter tarsi.

Plumage coloration and ambient temperatures

Long-term study

Number of breeding Grey females from 1987 to 2000 was greater in years when spring/summer temperatures were lower (ANCOVA with temperatures as a dependent variable, number of Grey females as a first covariate: $F_{1,10} = 9.91$, $P = 0.01$; number of Red-Grey females: $F_{1,10} = 0.15$, $P = 0.70$; number of Red females: $F_{1,10} = 1.40$, $P = 0.26$; Fig. 2). Winter temperatures were not associated with number of Grey females (similar statistical model, $F_{1,10} = 0.53$, $P = 0.48$; Red-Grey: $F_{1,10} = 0.001$, $P = 0.97$; Red: $F_{1,10} = 0.06$, $P = 0.82$).

Plumage coloration, recapture probabilities and survival

Long-term study

Model selection based on AICc showed that the recap-

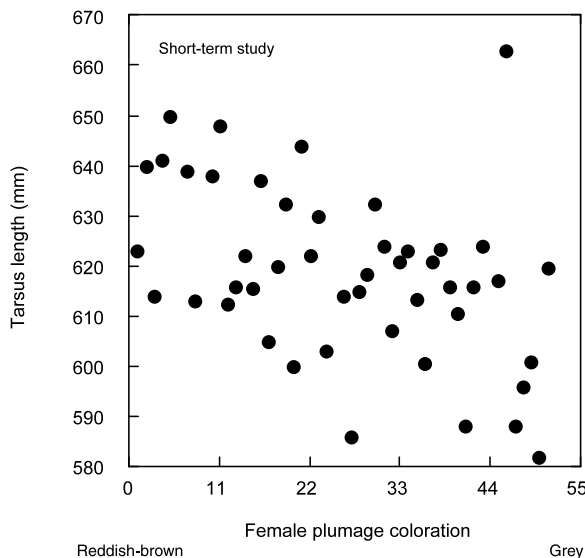


Fig. 1. Relationship between tarsus length and plumage coloration in females. Data are from the short-term study. Each individual appears only once.

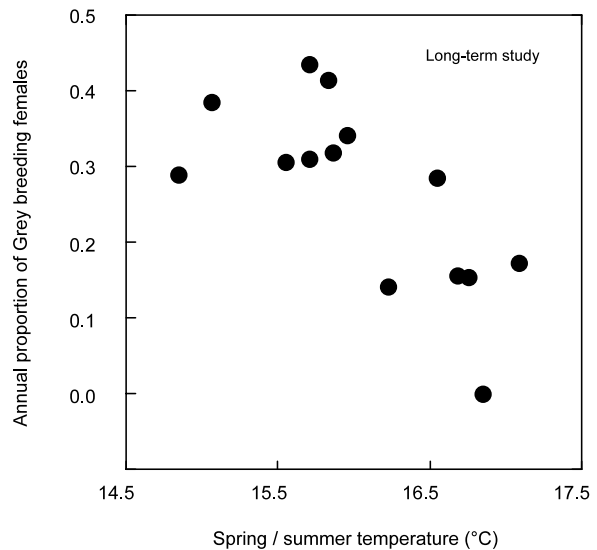


Fig. 2. Relationship between the annual proportion of Grey breeding females and spring/summer ambient temperatures. Data are from the long-term study. Pearson correlation is $r = -0.70$, $n = 14$ years, $P = 0.005$.

ture probabilities varied over the years and were lower for Grey than Red owls (model 5, Table 4). This suggests that Grey owls skip reproduction in poor years, as further supported by the observation that the proportion of Red breeding females was greater in years when the total number of breeding pairs was smaller ($r = -0.66$, $n = 14$, $P = 0.01$; Fig. 3). The estimated recapture probabilities ranged from 0.07 (SE = 0.04) to 0.71 (SE = 0.12) in Grey individuals, from 0.11 (SE = 0.05) to 0.79 (SE = 0.10) in Red-Grey individuals, and from 0.17 (SE = 0.07) to 0.86 (SE = 0.08) in Red individuals. Survival was best described by a model assuming constant survival over the years (model 5), and this model was supported by 41% of the data (Akaike weight). The estimated mean annual survival rate was 0.73 (SE = 0.02). AICc showed that all other models were relatively poorly supported by the data. Specifically, we found no support for the hypothesis that survival of Grey, Red-Grey and Red breeding females differed (model 7), or that females displaying a different colour type differentially survived under different population densities (model 8).

Plumage coloration and reproductive success

Long-term study

To examine whether offspring from differently coloured females differed in body mass, we plotted a second-order curve between the \log_{10} -transformed mean nestling body mass and the \log_{10} -transformed mean nestling wing length (Fig. 4; data from nestlings raised in the

Table 4. Summary of model selection for the capture-mark-recapture analysis of annual survival (ϕ), and recapture probabilities (P). The subscripts denote the factors included in a particular model. We analysed survival and recapture in relation to year (y), colour morph (c), breeding population density (dens), and their two way interactions, symbolised by *. A placeholder, '.' denotes the constant (intercept only) model. We run all models in program MARK (White and Burnham 1999), and followed basic capture-mark-recapture methodology for model selection (Lebreton et al. 1992). The fit of the models is assessed by Akaike's Information Criterion (AICc), where a lower value shows better fit. Delta AICc gives the difference in AICc between the current model and the best model (in bold); the Akaike weights assess the relative support that a given model has from the data, compared to the other models in the set; Num. Par is the number of parameters of a given model. Finally, the Deviance is the difference in $-2 \log$ Likelihood between the current model and the saturated model, where the saturated model is the one where the number of parameters equals the sample size. Data from the long-term study.

	Model	AICc	Delta AICc	Akaike Weights	Num. Par	Deviance
1	$\phi_{y,c,y*c} P_{y,c,y*c}$	999.399	82.182	0.000	75	368.848
2	$\phi_{y,c,y*c} P_{y,c}$	938.655	21.438	0.000	38	408.247
3	$\phi_y P_{y,c}$	929.446	12.229	0.001	27	425.070
4	$\phi_y P_{y,c}$	963.427	46.210	0.000	14	487.946
5	$\phi_{y,c} P_{y,c}$	917.217	0.000	0.408	15	439.581
6	$\phi_{y,c} P_{y,c}$	931.301	14.084	0.000	28	424.620
7	$\phi_c P_{y,c}$	918.856	1.639	0.180	16	439.053
8	$\phi_{dens,c,dens*c} P_{y,c}$	920.691	3.474	0.072	18	436.524
9	$\phi_{dens+c} P_{y,c}$	919.896	2.679	0.107	17	437.916
10	$\phi_{dens} P_{y,c}$	918.339	1.122	0.233	16	438.536

same nest were averaged). The equation for this curve is given by $\log \text{Mass} = -0.375 + 2.352 \times \log \text{Wing} - 0.47 \times (\log \text{Wing})^2$ ($F_{1,352} = 610.12$, $P < 0.001$), and the residuals indicate whether the nestlings were relatively heavy (positive residuals) or light (negative residuals) independent of age. Nestlings of differently coloured females did not differ in residual body mass (one-way ANOVA in which mean residual body mass value was calculated for each breeding female: $F_{2,163} = 1.0$, $P = 0.37$; two-way ANOVA with year entered as a factor, colour type: $F_{2,299} = 0.31$, $P = 0.73$, year: $F_{13,299} = 2.38$, $P = 0.005$). Female plumage coloration was not significantly associated with mean hatching date (each female appears only once in this one-way ANOVA: $F_{2,167} =$

0.47, $P = 0.62$) or mean brood size ($F_{2,180} = 0.15$, $P = 0.86$). Individuals of the three colour types (Red, Red-Grey and Grey) produced a similar total number of offspring from 1987 to 2000 (on average 5.67 ± 5.34 chicks produced per female in 14 years, ANOVA: $F_{2,199} = 0.26$, $P = 0.77$).

Short-term study

Table 5 shows that in 1997 (Fig. 5a) and 1998 (Fig. 5b), but not in 1999, offspring of greyer females were heavier.

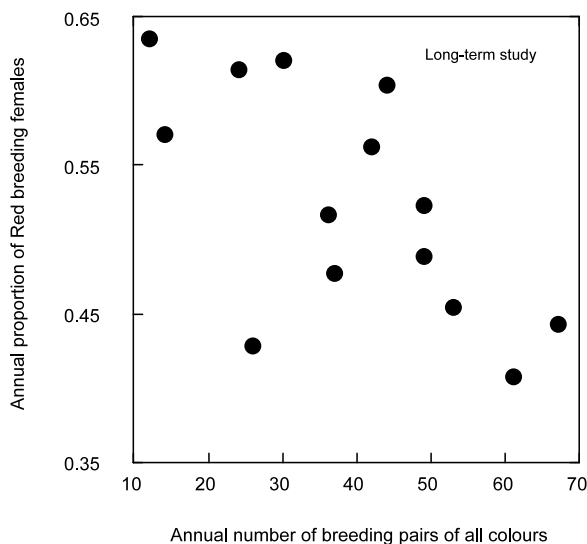


Fig. 3. Relationship between the annual proportion of all breeding females that were Red and the annual number of breeding pairs of all colours from 1987 and 2000. Data are from the long-term study.

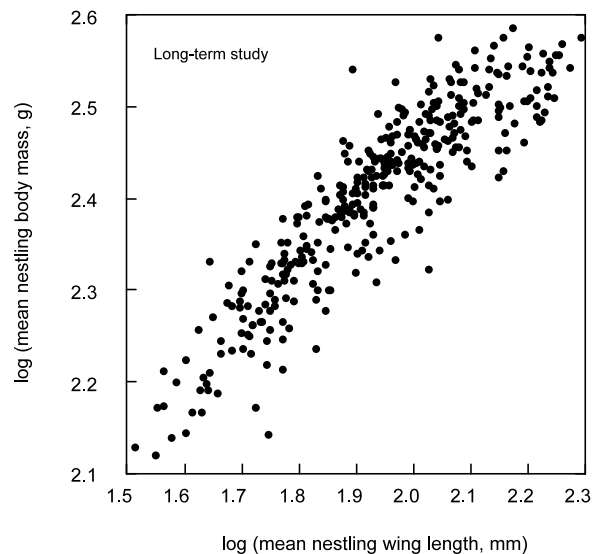


Fig. 4. Relationship between the \log_{10} -transformed mean nestling body mass and the \log_{10} -transformed mean nestling wing length. Only one data point per female is considered (mean values from all offspring raised in the same or different nest were calculated per female). Data are from the long-term study.

Table 5. Partial correlation analyses between female plumage coloration and nestling body condition, brood size and hatching date. Each partial correlation controls for the other variables presented in the Table. Data are from the short-term study. The symbol * denotes $P < 0.05$ and ** denotes $P < 0.02$.

	1997 (n = 15 nests)	1998 (n = 27)	1999 (n = 27)
Nestling body condition	$r_{\text{part}} = 0.62^{**}$	$r_{\text{part}} = 0.42^*$	$r_{\text{part}} = 0.16$
Brood size	$r_{\text{part}} = 0.16$	$r_{\text{part}} = -0.31$	$r_{\text{part}} = 0.34^*$
Hatching date	$r_{\text{part}} = 0.30$	$r_{\text{part}} = -0.18$	$r_{\text{part}} = 0.28$

Discussion

Interpretation of the results

In the short-term study, offspring of greyer females were heavier than those of redder females, whereas in the long-term study we did not find such a relationship. The latter result is difficult to interpret because at least four persons measured wing length, and in 2002 it appeared that there was a non-negligible variation in the way these four persons worked. Combined with the fact that plumage coloration was not measured with an accurate continuous scale, measurement errors may potentially explain the absence of any significant association between offspring body condition and female plumage coloration. In the short-term study, we calculated residuals from the regression of nestling body mass on nestling wing length to estimate nestling body mass independently of age. This procedure is reliable, since wing length is not correlated with plumage coloration (for a similar result see also Baudvin and Dessolin 1992). The residuals indicated that the off-

spring of greyer females were on average heavier although greyer females may produce chicks with smaller bones (tarsi were smaller in greyer females).

The relationship between nestling body condition and mother plumage coloration may reflect the fact that greyer females (1) occupy habitats of a higher quality, (2) invest (or mates invest; see Roulin 1999 for such a case in the barn owl) more effort in the rearing of their offspring, (3) bias sex-ratio towards daughters (since females are 1.3 times heavier than males but only 1.04 times larger; Baudvin and Dessolin 1992). Alternatively, the metabolism of offspring of grey and red females may differ (e.g. Mosher and Henny 1976). Whatever the reason, the absence of a strict disassortative pairing with respect to plumage coloration indicates that the correlation between female plumage coloration and nestling body condition is probably not inflated by male plumage coloration. Greyer females may therefore achieve higher fitness by producing higher quality offspring. Under this scenario, and assuming that the expression of plumage coloration is heritable, as is the case in the closely related species *Otus asio* (Hasbrouck 1893, Hrubant 1955) and *Tyto alba* (Roulin et al. 1998, Roulin and Dijkstra 2003), reddish-brown females should be selected against and disappear from the populations we studied. We therefore require a mechanism to explain the plumage polymorphism. Results from the long-term study provide a plausible solution. In years when the number of breeding pairs was lower, the proportion of Red breeding females was greater. Capture-mark-recapture analyses indicate that this is not due to the fact that Red females survive better in such years but because the non-breed-

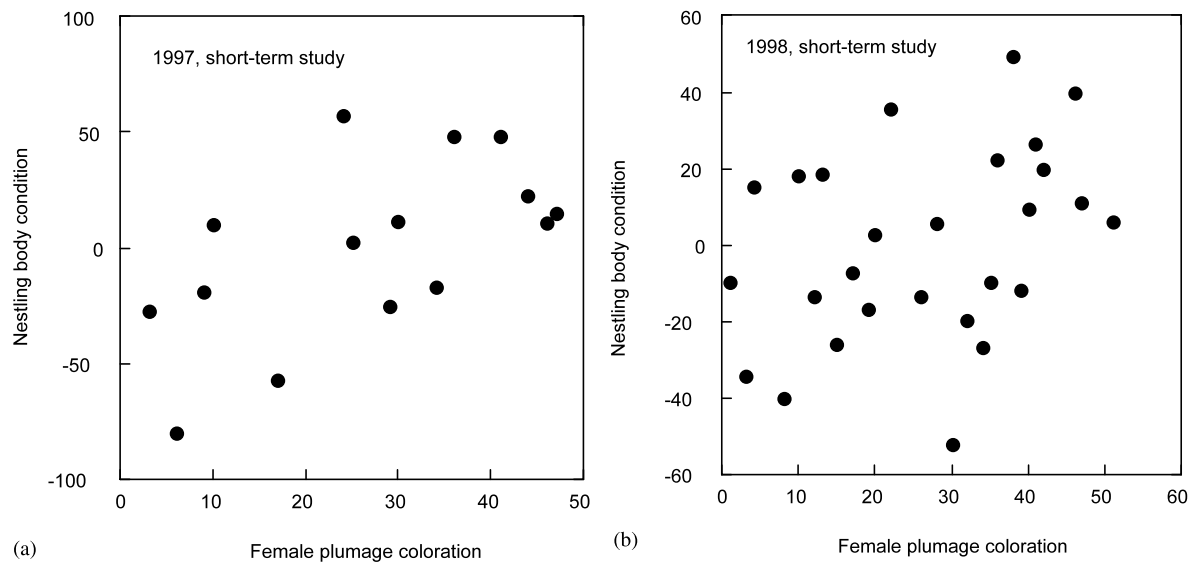


Fig. 5. Relationship between nestling body condition and coloration of the mother in 1997 (a) and 1998 (b). Body condition is defined as the residuals of the regression of mean nestling body mass on mean nestling wing length. In 1997 the Pearson correlation between body condition and coloration is $r = 0.59$, $n = 15$ nests, $P = 0.020$ and in 1998 $r = 0.36$, $n = 27$ nests, $P = 0.068$. Data are from the short-term study.

ing section of the population consists mainly of Grey females. This scenario does not exclude a role of gene flow from incoming reddish-brown females potentially compensating for the reduced reproductive success of such females in our study area, but also of frequency-dependent reproductive success.

Why is plumage coloration correlated with fitness components and ambient temperature?

Results from the present study are consistent with Galeotti and Cesaris's (1996) finding that Italian grey tawny owls suffered a higher mortality in warm years. Therefore, covariation between plumage coloration, ambient temperature and reproductive success may not only be found in Switzerland but also in other populations, and hence may be of general applicability. This should be relatively easily tested, since the tawny owl is a popular study species among ornithologists. However, the correlation between ambient temperature and some colour-dependent life-history components might be spurious and caused by an unknown correlated variable. If ambient temperature causally affected colour-dependent mortality and the propensity to breed, we should have expected that Grey females breed at higher altitude than Red females. Results from both the long- and short-term studies, as well as the study of Galeotti and Cesaris (1996), showed that there is no relationship between plumage coloration and altitude. Furthermore, there is no evidence that plumage coloration varies clinally in Europe with Grey birds being not more frequent in northern than southern European parts (Galeotti and Cesaris 1996).

The greatest challenge now is to understand how the relationships reported in our study can arise. As said above, variation in plumage coloration probably has a very strong genetic component as already demonstrated in two other owl species (*Otus asio*: Hasbrouck 1893, Hrubant 1955, *Tyto alba*: Roulin et al. 1998, Roulin and Dijkstra 2003). Since in a closely related owl species grey and red individuals showed different oxygen uptake (Mosher and Henny 1976), genes coding for plumage coloration may have pleiotropic effects on a variety of attributes leading grey and red individuals to have different life-history tactics. Detailed physiological studies are therefore required to investigate how such pleiotropic effects can take place and this may also help determine the full range of physiological and ecological correlates of plumage coloration. We can indeed expect that differently coloured females live in a different environment, have a different diet and behave differently, since redder females had longer tarsi. The tawny owl therefore appears to be a promising species for further studies on the evolution and function of plumage variation for which variation has a strong underlying genetic basis.

Acknowledgements – B. Ducret and A. Roulin are grateful to Anne-Lyse Ducrest, the late Martin Epars, Henri Etter and Pierre-André Fragnière for their help during the field work from 1997 to 1999. P.-A. Ravussin thanks Daniel Béguin, Lionel Maumary, Gaston Potterat and Daniel Troillet for their active participation in the fieldwork from 1987 to 2000. Data on ambient temperatures were kindly provided by the meteorological station of Bern (SMA). This paper was written during a post-doctorate financed by the Swiss Science Foundation to A. Roulin (grant no. 823A-064710) and to R. Altwegg (81ZH-68483). A previous version of the manuscript was improved by Tim Fawcett, Bruce Lyon and Peter Sunde. We warmly thank them.

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(Received 8 October 2002, revised 9 January 2003, accepted 7 February 2003.)