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GENETIC, ENVIRONMENTAL, AND CONDITION-DEPENDENT EFFECTS ON FEMALE AND MALE ORNAMENTATION IN THE BARN OWL *TYTO ALBA*

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Abstract.—Secondary sexual characters are thought to indicate individual quality. Expression of sex-limited traits in an extravagant state may require both the underlying genes and the available nutrient resources. The assessment of the relative contribution of genes, environment, and body condition is relevant for understanding to that extent the extravagant trait may signal genotypic or phenotypic quality of the individual. In birds, usually only the males are ornamented. In the barn owl, *Tyto alba*, both females and males display sex-limited plumage traits. Males are commonly lighter colored and females spottier. In an experiment with combined cross-fostering and brood size manipulation we determined the relative contribution of genes, environment, and body condition to the variation in plumage coloration and plumage spottiness. The partial cross-fostering experiment tested the relative importance of shared genes and a shared environment for the resemblance of related birds. Siblings raised in different nests converged toward similar trait values, offspring resembled the true but not the foster parents, and plumage traits of unrelated nestlings sharing the same nest were not correlated. Results were not inflated by maternal effects detectable in the mother's phenotype, because middaughter to mother resemblance was not higher than midson to father resemblance. This suggests that plumage coloration and spottiness are largely genetically inherited traits, and that the rearing environment does not have a strong impact on the expression of these traits. To further investigate whether the two sex-limited traits are condition dependent, brood sizes were manipulated. Enlargement or reduction of broods by two nestlings resulted in lower and higher body mass of nestlings, respectively. However, nestlings raised in enlarged or reduced broods did not show either a significantly darker or lighter or a more or less spotted plumage. We did not detect any genotype-by-environment interaction. In conclusion, simultaneous cross-fostering and brood size manipulation demonstrate that additive genetic variance for plumage coloration and spottiness is maintained and that both the rearing environment and body condition do not account for a large proportion of the phenotypic variance in female and male ornamentations.

Key words.—Condition-dependent plumage traits, environmental effects, genetic plumage polymorphisms, secondary sexual characters, *Tyto alba*.

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Experimental studies have shown that females prefer to mate with ornamented males (e.g., Andersson 1982; Møller 1988; Hill 1991). The type of benefits obtained from mate choice depends on the relative contribution of genes and the environment to the observed variance in ornamental extravagance (Gray 1996). When the preferred trait is heritable, females would produce more attractive sons (Fisher 1958) or the progeny would get viability-linked genes assuming that the ornament honestly signals genotypic quality (Hamilton and Zuk 1982; Møller 1990). When the preferred trait is mainly condition dependent, females may gain resources, for example, ornamented individuals may be healthier, and therefore potentially better parents (Hoelzer 1989; Hill 1991). The partitioning of the phenotypic variance into genotypic and environmental components is useful to assess the extent to which a trait expresses genotypic and phenotypic qualities. For instance, female peacocks (*Pavo cristatus*) produce chicks with the high survival prospect when mated to males displaying the most elaborate trains suggesting that ornamented males transmit "good genes" into offspring (Petrie 1994). In the case of the house finch (*Carpodacus mexicanus*), continuous variation in plumage coloration reflects differential access to carotenoid resources to develop the brighter trait, and brighter males are better fathers (Hill 1991, 1992).

The barn owl is especially suited to partition the phenotypic variance of plumage ornaments into genetic and environmental components and to test the effect of body condition on the expression of sex-limited traits. Nestlings and adults exhibit two different plumage traits, coloration and spottiness. Coloration varies from white to dark reddish brown, and spottiness varies from immaculate to heavily flecked. Both traits are sex limited in their expression (e.g., Lande 1987); males are lighter colored and less spotted than females (Taylor 1993; Roulin 1996a). These sexual dimorphisms are marked in all European populations, but in northern and eastern populations barn owls are generally darker and spottier than in southern and western populations, and birds in central Europe exhibit an intermediate form (Voous 1950). Because of gene flow between populations (Cramp and Simmons 1985) and nonassortative mating with respect to plumage characteristics (Baudvin 1975), most birds on the continent should have a more-or-less intermediate plumage. Thus, birds may be differently colored and spotted within and among populations for at least three not mutually exclusive reasons. First, plumage coloration and spottiness are genetic polymorphisms, and two possible mechanisms would maintain the phenotypic variation in plumage traits within populations. Each morph may provide frequency-dependent benefits to their bearers, that is, different plumage patterns provide equal pay-offs when each morph is displayed by the ESS-proportion of all individuals (Maynard Smith 1982; Lank et al. 1995). Also, birds may benefit by making their identity recognizable through individual plumage patterns (Whitfield 1988), which require a highly variable genetic system for the production of both ornamentations to ensure that every individual is different from others. Second, the expression of plumage coloration and spottiness depends on the environment, for example, the birds may vary in their

access to the resources necessary for the production of a white or reddish-brown coloration or for spot elaboration (Slagsvold and Lifjeld 1985; Hill 1994). Finally, the two traits may depend on some aspects of body condition influencing one or several allocation trade-offs within the individual (Møller 1989; Slagsvold and Lifjeld 1992; Gustafsson et al. 1995).

We conducted a partial cross-fostering experiment to test the respective importance of genetics and environment for the variation in plumage coloration and spottiness. To test for condition-dependence of plumage traits, we simultaneously designed a brood-size manipulation including enlarged and reduced broods. The experiment predicts for the genetic, environmental, and condition-dependent components of the variation in plumage ornamentation: (1) The genetic component: siblings raised in different nests will resemble each other, and offspring will resemble parents. This prediction is free of bias if there is no genotype-environment correlation (i.e., nestlings should not resemble foster parents) and if maternal effects detectable in the mothers' phenotypes are absent (e.g., heavily spotted females do not produce high-quality eggs that influences the daughters' spottiness). That is, daughters should not resemble mothers more than sons resemble fathers (Falconer 1989; Boag and van Noordwijk 1987). (2) The environmental component: unrelated nestlings sharing a common nest will be similarly ornamented (Falconer 1989). (3) The condition-dependent component: brood size manipulation will affect nestling ornamentation, that is, nestlings develop ornamentations differently under experimentally stressed or relaxed rearing conditions. Condition-dependence may be similarly expressed by all genotypes, or may vary among genotypes under the presence of a genotype-by-environment interaction (Falconer 1989).

Materials and Methods

The Study Organism

The barn owl, *Tyto alba*, includes several subspecies distributed throughout the world. It is a long-lived and medium-sized bird that hunts during the night, mainly on small mammals using auditory cues. Owls breed in cavities of trees and cliffs, houses, and nestboxes. This bird is characterised by a great variability in clutch size (mean: 5 to 6; range: 2 to 18 eggs) by the production of one or two clutches per year (Taylor 1994) and the frequent occurence of brood reduction and cannibalism (Baudvin 1978). Fluctuations in prey abundance have strong effects on population dynamics, laying dates, and reproductive success. Both males and females can be polygynous (Roulin 1996b). They often shift nestboxes and change mates between two breeding attempts (unpubl. data). Post-fledging dispersal varies from some movements of less than one kilometer up to more than 1000 km. Adults are mostly sedentary, but between two breeding attempts females sometimes move several hundred kilometers (unpubl. data). Barn owls suffer high mortality during cold winters (Taylor 1994).

Experimental Design

We carried out the study in 1996 in the Broye Plain, western Switzerland. The study area covers 190 km^2. Barn owl pairs bred in nestboxes fastened on barns. We checked nests at regular intervals to record clutch sizes, hatching success, age of each chick using wing length (Schönfeld and Girbig 1975; Taylor 1993), and the number of fledglings. We captured adults at the nest and distinguished females from males by the presence of a brood patch (Cramp and Simmons 1985). We determined age from leg bands when birds were banded some years ago or by checking the moult pattern of the primaries and secondaries. Feathers of first-year individuals are all of the same generation and not abrased (Baker 1993; Taylor 1993).

We enlarged 28 randomly chosen broods (E), and reduced 28 others (R) by two zero- to five-day-old nestlings. To manipulate brood sizes, we removed one randomly chosen nestling from an E-nest and placed it in an R-nest. From an R-nest, we removed three randomly chosen nestlings and put them in an E-nest (Fig. 1). In this way, we simultaneously did a cross-fostering and a brood size manipulation, that is, all nests contained cross-fostered and non-cross-fostered nestlings, and we enlarged or reduced the E- and R-nests by two nestlings, respectively (Table 1). For unknown reasons, parents subsequently abandoned four enlarged and two reduced nests. Before banding we indentified the origin of the owlets with nontoxic, waterproof ink markings. We marked cross-fostered nestlings and their genetically unrelated new nestmates with different colors. Because of a strong hatching asynchrony in natural broods, a size hierarchy within the brood arises where the youngest chicks show slower growth rates (Wilson et al. 1986) and suffer high mortality (Baudvin 1978; unpubl. data). Thus, if the two ornamentations are condition-dependent traits, a brood size manipulation may differently affect nestlings placed at the top and bottom of this hierarchy (Table 1). To test this possibility, we assigned rank 1 to the eldest nestling, rank 2 to the second nestling, and so on, and compared nestlings placed above the median rank in enlarged versus reduced broods and did the same for nestlings below the median rank.

The Assessment of Plumage Ornamentation

One of us (AR) recorded the two plumage characteristics on the breast, belly, flanks, and underside of the wings in adults and 55-day-old nestlings. AR scored coloration by comparison to eight color chips from I for dark reddish-brown to VIII for white. In the color Atlas of Mecanorma (normacolor spatial system™; Mecanorma International, 78610 Le Perray-en-Yvelines, France), color score I corresponds to the color chip L*60C*40h60, II to L*70C*40h60, III to L*80C*30h70, IV to L*85C30h70, V to L*90C10h70, VI to L*90C*20h80, VII to L*95C*10h80, and VIII to white. For statistical analyses, we calculated for each bird the mean color score from the four body parts. To measure plumage spottiness on the same four body parts, AR counted the number of spots within a 60 × 40 mm frame, and determined the diameter of three to 15 representative spots to the 0.10 mm with a calliper. For each body part we calculated the mean spot diameter and the proportion of the surface covered by spots using the following formula: $100 \times (\pi \times \text{number of spots} \times [\text{mean spot diameter}/2]^2)/(60 \times 40)$. We averaged the values of the two flanks, respectively, of the two wings. For statistical analyses we calculated, for each bird, the mean

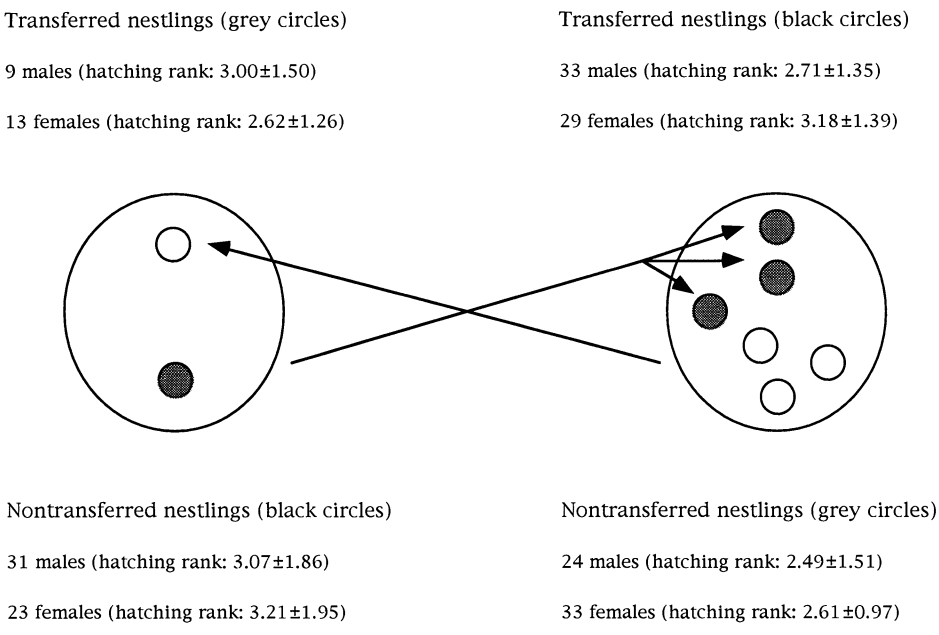

FIG. 1. Design of the simultaneous cross-fostering and brood-size manipulation. Black and grey circles represent nestlings of different origin. Three nestlings were transferred from R-nests to E-nests, but only one nestling from E-nests to R-nests. The mean hatching rank (± 1 SD) is given for transferred and nontransferred nestlings. For each brood, rank 1 was assigned to the first hatched nestling.

spottiness value from the four body parts. AR took blind measurements of plumage characteristics with respect to the sex and origin of the bird, because at that time sex and origin was unknown to the observer. To estimate the repeatability of the method of assessing coloration and spottiness, we took measurements of 27 nestlings at 55 and 62 days of age and of 65 adults at the 20th day of incubation and when the eldest nestling was 25 days old. Correlations between the first and second measures are significant for both plumage coloration (nestlings: Spearman rank correlation, $r_s = 0.87$, $n = 27$, $P < 0.001$; adults: $r_s = 0.95$, $n = 65$, $P < 0.001$) and plumage spottiness (nestlings: Pearson product-moment correlation, $r = 0.97$, $n = 27$, $P < 0.001$; adults: $r = 0.90$, $n = 65$, $P < 0.001$); measurement errors may therefore be negligible.

Sexing Method of Nestling

We determined the sex of the nestlings by one of the following two methods. One of us (HR) inspected the gonads by laparoscopy on 75 nestlings from 39 randomly chosen families (69 nestlings were from experimental broods, and six nestlings from broods not used in the experiment, Table 1). For further details and effects of laparoscopy on the individual bird see Richner (1989). AR measured 10 sexually dimorphic traits (length of bill, length of hind claw, breast, belly, flank and wing coloration and spottiness) when birds were 55 days old. Because color scores of the four body regions are strongly correlated ($r_s = 0.86$–0.93), as are spottiness values ($r = 0.77$–0.91), we used only the most sexually dimorphic breast coloration and belly spottiness in a dis-

TABLE 1. Number of nestlings and sex ratio (proportion of males) in 26 reduced and 24 enlarged broods before and after the brood size manipulation, based on the sexing by endoscopy or by discriminant function analysis. Number of nestlings sexed and percentage of nestlings at the top of the size hierarchy after the brood size manipulation.

Treatment	Before manipulation		After manipulation	
	Reduced	Enlarged	Reduced	Enlarged
Number of nestlings	5.65 ± 1.41	5.04 ± 1.16	3.65 ± 1.41	7.04 ± 1.16
% females at the top of the size hierarchy	·	·	49	53
% males at the top of the size hierarchy	·	·	50	46
Nestlings sexed by endoscopy	·	·	23	46
Nestlings sexed with discriminant function	·	·	55	71
Sex ratio	0.59 ± 0.30	0.42 ± 0.35	0.55 ± 0.28	0.49 ± 0.29

criminant function analysis for segregating the two sexes. A model with simultaneous inclusion of the following four variables gave a canonical loading for belly spottiness of 0.73, breast coloration −0.57, bill length 0.47, and length of hind claw 0.17. In a cross-validation procedure assessing the reliability of the discriminant function, we calculated a discriminant function from 74 birds of known sex and then classified the remaining nestling based on the model generated. We repeated this procedure 75 times, always leaving out another individual. On average, the sex of five males and five females was wrongly attributed, giving 87% correct discrimination. To sex 126 other nestlings, we used a discriminant function based on the 75 nestlings (Table 1).

Statistical Procedure

For all statistical analyses of plumage coloration and plumage spottiness, we calculated the mean value from all nestlings within given classes (e.g., sisters raised in a same nest, brothers at the top of the size hierarchy, etc.). Thus, we consider data points in a given test as independent, and large families have the same weight in the analyses as small ones. For parent-offspring comparisons we considered only yearling breeding birds, because plumage ornamentation can change from the first to the second year of age but not between fledging and the end of the first year (Roulin 1996a; unpubl. data). We evaluated normality by a Lilliefors test (Wilkinson 1989). We normalized distributions of plumage spottiness values by square-root transformation and performed parametric analyses. Color score distributions deviated from a normal distribution even after log and square-root transformations. Therefore, we used nonparametric analyses for plumage coloration. Because heritabilities based on small sample sizes are likely to be unreliable (Boag and van Noordwijk 1987), we did not calculate heritability estimates. Instead, we performed correlation analyses to assess whether plumage ornamentations are genetically and environmentally determined. We performed analyses using the SYSTAT statistical package (Wilkinson 1989). Significance values are two-tailed with a 0.05 significance level.

RESULTS

Genetic and Environmental Effects on Plumage Ornamentation: Cross-Fostering Experiment

I. Sibling Comparison

Phenotypic variation in plumage ornamentation has a genetic basis because brothers raised in different nests resembled each other (color: $r_s = 0.55$, $n = 26$, $P < 0.005$; spottiness: $r_s = 0.56$, $n = 26$, $P = 0.003$; Fig. 2a,b). For sisters, the correlation was significant for plumage spottiness ($r_s = 0.54$, $n = 19$, $P = 0.017$; Fig. 2d), but not for plumage coloration ($r_s = 0.19$, $n = 19$, $P > 0.20$; Fig. 2c).

The environment had no detectable effect on plumage ornamentation, because nonrelative male nestlings raised in the same nest did not converge toward similar trait values (color: $r_s = 0.06$, $n = 19$, $P > 0.50$; spottiness: $r = 0.30$, $n = 19$, $P = 0.21$; Fig. 3a,b). The same conclusion applies for nonrelative female nestlings (color: $r_s = -0.09$, $n = 21$, $P > 0.50$; spottiness: $r = 0.17$, $n = 21$, $P = 0.46$; Fig. 3c,d). There was no apparent effect of the brood size treatment (open and closed symbols in Fig. 3).

II. Parent-Offspring Comparison

Plumage traits of nestlings and same-sex foster parent were not significantly correlated (males: color: $r_s = 0.48$, $n = 9$, $P = 0.20$; spottiness: $r = 0.22$, $n = 9$, $P = 0.57$; females: color: $r_s = -0.65$, $n = 7$, $P > 0.10$; spottiness: $r = -0.13$, $n = 7$, $P = 0.79$) suggesting that there was no genotype-by-environment correlation increasing the resemblance of related individuals. Thus, by comparing the midtrait value of siblings raised in the foster nest or the nest of origin with the trait value of the true parent, we tested whether phenotypic variance in plumage coloration and plumage spottiness has an additive genetic component. Correlations of mid-son versus father plumage ornamentations were significant (color: $r_s = 0.73$, $n = 15$, $P < 0.002$; spottiness: $r = 0.58$, $n = 15$, $P = 0.023$; Fig. 4a,b). Correlation of mid-daughter versus mother was significant for plumage spottiness ($r = 0.55$, $n = 16$, $P = 0.026$), but not for plumage coloration ($r_s = 0.35$, $n = 16$, $P = 0.20$; Fig. 4c,d). The mid-daughter versus mother relationships were not stronger than the mid-son versus father relationships, suggesting that maternal effects detectable in the mother's phenotype did not inflate the parent-offspring resemblance.

Condition-Dependent Effect on Plumage Ornamentation: Brood Size Manipulation Experiment

I. Comparison among Families

The brood-size manipulation affected body mass of nestlings as measured at the age of 25 and 55 days after hatching: Nestlings in enlarged broods had a significantly lower body mass than nestlings in reduced broods (repeated measures ANOVA; brood size treatment: $F_{1,48} = 10.22$, $P = 0.002$; Table 2). The brood-size manipulation experiment is therefore useful for testing if the expression of plumage ornamentations is condition dependent. Condition dependence predicts that the cross-fostered, unrelated nestlings raised in enlarged or reduced nests will differ in the expression of plumage characteristics. All these nestlings are raised by foster parents and are therefore randomized for both the brood-size treatment and the environment. Plumage traits of male nestlings from enlarged and reduced broods did not differ significantly (median coloration: 6.25 and 6.75, respectively, Mann-Whitney test, $U = 117$, $n = 18, 10$, $P = 0.19$; mean spottiness: 1.15 ± 0.49 (SD) and 1.28 ± 0.56, Student t-test, $t = -0.63$, df = 26, $P = 0.54$). The same holds for female nestlings (median coloration: 5.00 and 5.75, $U = 135$, $n = 19, 12$, $P = 0.40$; mean spottiness: 2.17 ± 0.59 and 2.22 ± 0.45, $t = -0.18$, df = 29, $P = 0.86$). As shown in this comparison of cross-fostered nestlings, there was no detectable treatment effect on plumage ornamentation among families.

Performing the same analysis on non-cross-fostered nestlings gives essentially the same result: unrelated nestlings had similar plumage ornamentations in enlarged as in reduced broods (males: median coloration: 6.72 and 6.50, respectively, $U = 107$, $n = 14, 21$, $P = 0.17$; mean spottiness: 1.14

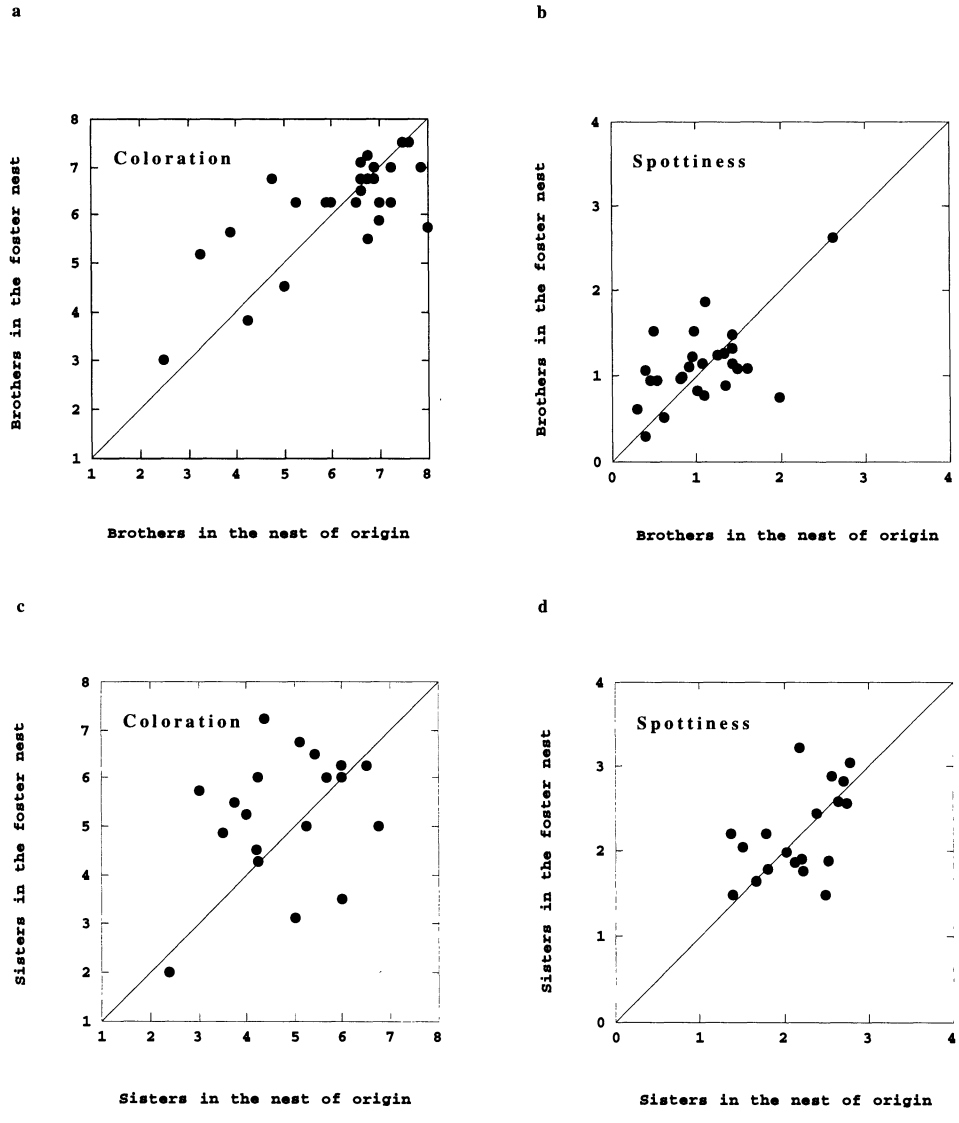

FIG. 2. Mean plumage coloration and spottiness of same-sex siblings raised in different nests. (a) Coloration of brothers. (b) Spottiness of brothers. (c) Coloration of sisters. (d) Spottiness of sisters. Each data point shows the mean trait value of siblings raised by true parents (X-axis) and the mean value of their siblings raised by foster parents (Y-axis). Data points on the diagonal represent relatives that were on average equally ornamented. Plumage ranges from dark reddish-brown (I) to pure white (VIII), and from unflecked (0) to strongly spotted (IV).

$\pm$ 0.51 (SD) and 1.27 $\pm$ 0.58, $t = -0.80$, df = 33, $P = 0.43$; females: median coloration: 5.00 and 5.00, $U = 171$, $n = 19, 17$, $P = 0.75$; mean spottiness: 1.93 $\pm$ 0.48 and 2.00 $\pm$ 0.49, $t = -0.44$, df = 34, $P = 0.66$). Plumage traits of cross-fostered and non-cross-fostered nestlings were not significantly different within treatments for both males (reduced broods: color: $U = 73$, $n = 10, 21$, $P = 0.17$; spottiness: $t = -0.05$, df = 29, $P = 0.96$; enlarged broods: color: $U = 160$, $n = 18, 14$, $P = 0.20$; spottiness: $t = -0.20$, df = 30, $P = 0.85$) and females (reduced broods: color: $U = 79$, $n = 12, 17$, $P = 0.31$; spottiness: $t = -1.28$, df = 27, $P = 0.21$; enlarged broods: color: $U = 146$, $n = 19, 19$, $P = 0.31$; spottiness: $t = -1.38$, df = 36, $P = 0.18$). Thus, there was no detectable effect of the cross-fostering per se on the results of the brood size manipulation regarding condition dependence of plumage ornamentations among families.

II. Comparison within Families

Plumage ornamentations of brothers from the two brood-size treatments were not significantly different (color: Wilcoxon matched-pairs signed-rank, $z = 1.17$, $n = 23$, $P = 0.24$; spottiness: paired t-test, $t = 1.32$, df = 22, $P = 0.20$; Fig. 5a,b). The same was true for plumage spottiness in sisters (spottiness: $t = -1.06$, df = 18, $P = 0.30$; Fig. 5d), but sisters tended to be lighter colored in enlarged than in reduced broods (color: $z = -1.80$, $n = 19$, $P = 0.07$; Fig. 5c). These results were probably not blurred by potential genotype-by-

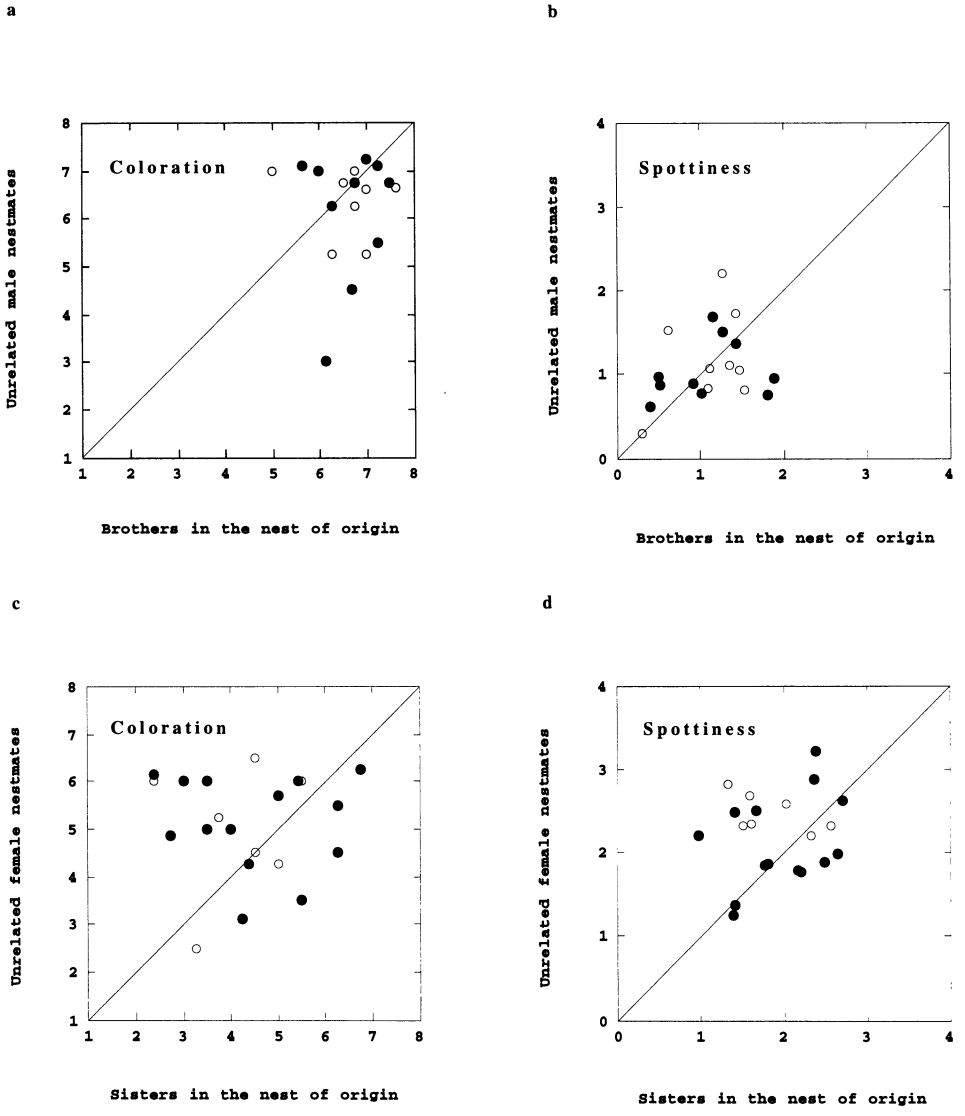

FIG. 3. Mean plumage coloration and spottiness of same-sex unrelated nestlings raised in same nest. (a) Coloration of male nestlings. (b) Spottiness of male nestlings. (c) Coloration of female nestlings. (d) Spottiness of female nestlings. Each data point shows the mean trait value of siblings raised by true parents (X-axis) and the mean value of their unrelated nestmates (Y-axis). Open and closed circles represent nestlings raised in enlarged and reduced broods, respectively.

environment interaction, because the difference in plumage characteristics of siblings raised in enlarged versus reduced broods was not significantly correlated with the plumage characteristics of the same-sex, true parent after correcting for sex effects (color: $tau = -0.28$, $n = 13$, $P > 0.10$; spottiness: $r_{partial} = -0.30$, $n = 13$, NS; Fig. 6a,b).

The body mass of the nestlings placed at the bottom of the size hierarchy was not significantly lower in enlarged than in reduced broods (repeated measures ANOVA, brood-size treatment: $F_{1,46} = 1.32$, $P = 0.26$), but nestlings at the top of the size hierarchy had a significantly lower body mass in enlarged broods ($F_{1,45} = 15.16$, $P < 0.001$; Table 2). Thus, if nutritional condition in the nest affects the expression of the two plumage ornamentations, siblings raised at the top of the size hierarchy should be differently ornamented in enlarged and reduced nests. However, we found no significant differences for either brothers (median coloration: 7.13 and 6.50, respectively, $z = 1.02$, $n = 8$, $P = 0.31$; mean spottiness: 0.86 ± 0.34 (SD) and 0.94 ± 0.35, $t = 0.50$, df = 7, $P = 0.63$), or sisters (median coloration: 5.25 and 5.63, $z = -1.06$, $n = 12$, $P = 0.26$; mean spottiness: 2.21 ± 0.55 and 2.31 ± 00.38, $t = 0.65$, df = 11, $P = 0.53$). Plumage of brothers placed at the bottom of the brood-size hierarchy was similar in the two treatments for both coloration (median: 6.25 in both treatments, $z = -0.31$, $n = 11$, $P = 0.76$), and spottiness (0.98 ± 0.43 and 0.99 ± 0.53, $t = 0.05$, df = 10, $P = 0.96$). Sample size for sisters placed at the bottom of the hierarchy was too small for reliable testing ($n = 5$ families). Because no statistical comparison was significant, we conclude that within families brood size manipulation had no detectable effect on the expression of plumage ornamentation of nestlings.

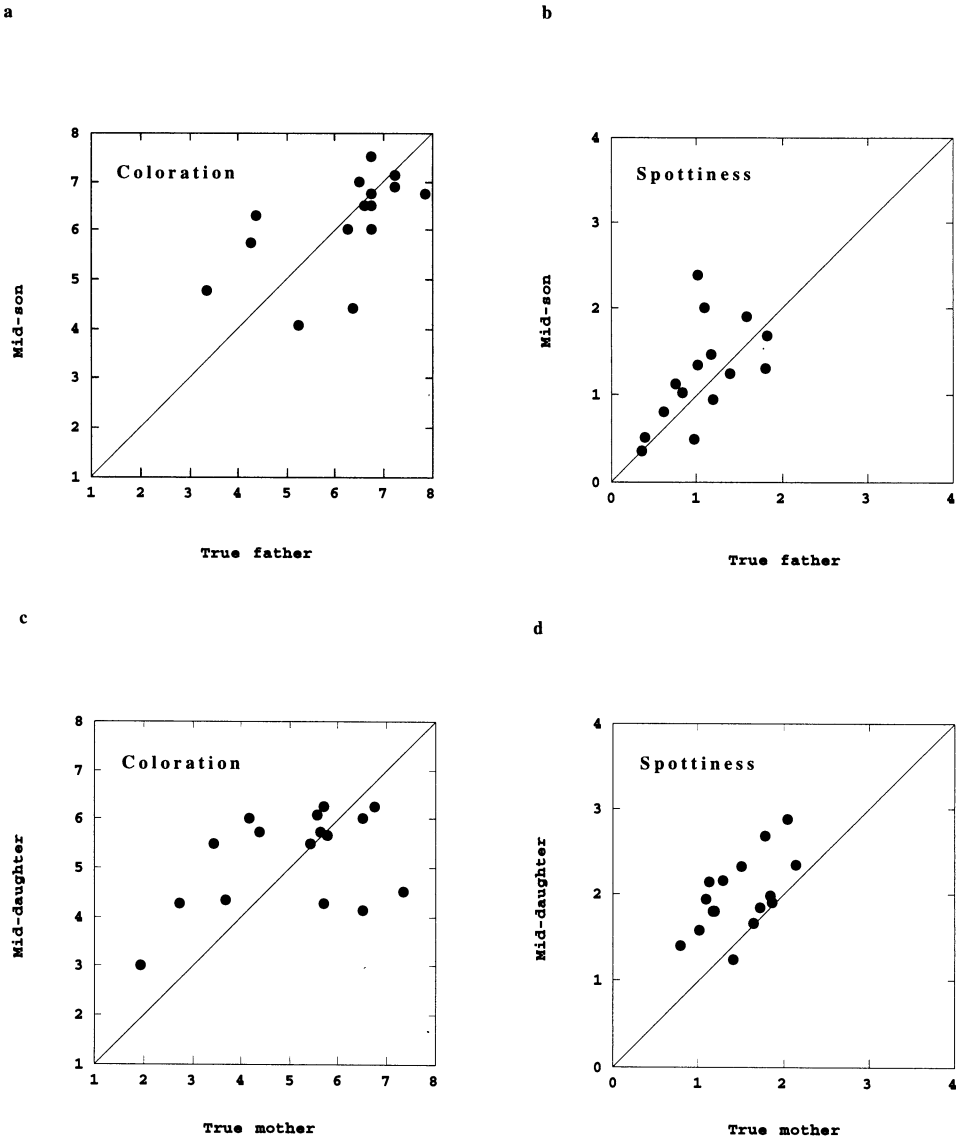

FIG. 4. Plumage ornamentation of midoffspring and same-sex true parent. (a) Mid-son-father plumage coloration. (b) Mid-son-father plumage spottiness. (c) Mid-daughter-mother plumage coloration. (d) Mid-daughter-mother plumage spottiness.

DISCUSSION

To our knowledge, this is the first study that addresses the simultaneous effects of genetics, environment, and body condition on the elaboration of multiple plumage ornaments. An experiment with simultaneous cross-fostering and brood size manipulation separated these three potential components responsible for the phenotypic variance in plumage coloration and spottiness. The study shows that the two plumage ornamentations are mainly genetically inherited, because siblings raised in different nests converged toward similar trait values and offspring resembled parents. Parental effects (genetic-environment correlation) and maternal effects detectable in the mother's phenotype did not inflate these results. The environment did not seem to have an impact on the production of plumage traits, because unrelated nestlings did not resemble each other as a consequence of sharing the same nest. Although brood size manipulation affected body mass of the nestlings, it did not affect the expression of the two ornamentations. We did not detect any genotype-by-environment interaction.

Environmental and Condition-Dependent Effects on Plumage Ornamentation

From the point of view of the "good-gene" and "good-parent" models of sexual selection (Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Andersson 1986; Hoelzer 1989), secondary sexual dimorphism evolved as honest advertisements of individual quality. To reinforce honesty, signals should be either costly to produce (Møller 1989; Hill and Montgomerie 1994; Swaddle and Witter 1994; Gustafsson et al. 1995) or to maintain (Rohwer and Rohwer 1978; Møller and de Lope 1994). The fact that nonrelatives

TABLE 2. Nestling body mass (g) at 25 and 55 days of age in reduced and enlarged nests. Means ± 1 SD.

	Overall mean		Nestlings at the top of the size hierarchy		Nestlings at the bottom of the size hierarchy	
Treatment	Reduced	Enlarged	Reduced	Enlarged	Reduced	Enlarged
25 days of age	302 ± 19	286 ± 18	318 ± 19	301 ± 22	290 ± 32	276 ± 40
55 days of age	346 ± 22	334 ± 20	349 ± 23	331 ± 23	343 ± 30	336 ± 23

sharing a common environment did not develop similar ornamentations, as shown by the cross-fostering experiment, indicates that the parents did not directly collect pigments or their precursors for reddish-brown and black colorations (Slagsvold and Lifjeld 1985; Hill 1992). The fact that the brood size manipulation did not affect ornamentations suggests that there is no trade-off between growth and metabolic transformation of the ingested food into reddish-brown or black pigments (Andersson 1986; Gray 1996). Even if the production of ornamentations at the nestling stage is free of costs, the change in ornamentation between the first and second year of age (Roulin 1996a; unpubl. data) may nevertheless be condition dependent. At this stage other trade-offs may control the expression of plumage ornamentation, as

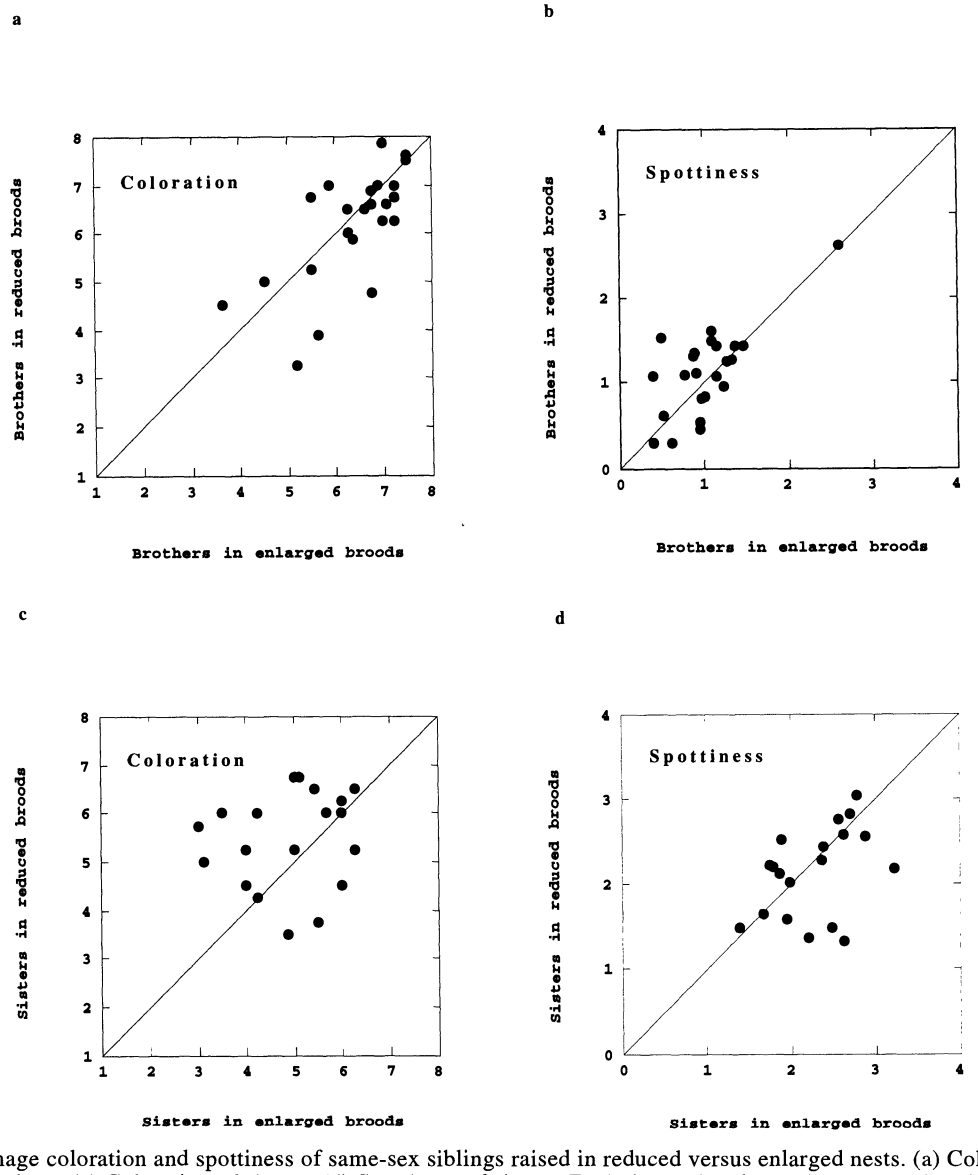

FIG. 5. Mean plumage coloration and spottiness of same-sex siblings raised in reduced versus enlarged nests. (a) Coloration of brothers. (b) Spottiness of brothers. (c) Coloration of sisters. (d) Spottiness of sisters. Each data point shows the mean trait value of siblings raised in an enlarged nest (X-axis) and the mean value of their siblings raised in a reduced nest (Y-axis). Data points below, on, and above the diagonal represent nestlings in reduced broods that were less, equally, or more lightly coloured (or spotted), respectively, than siblings in enlarged broods.

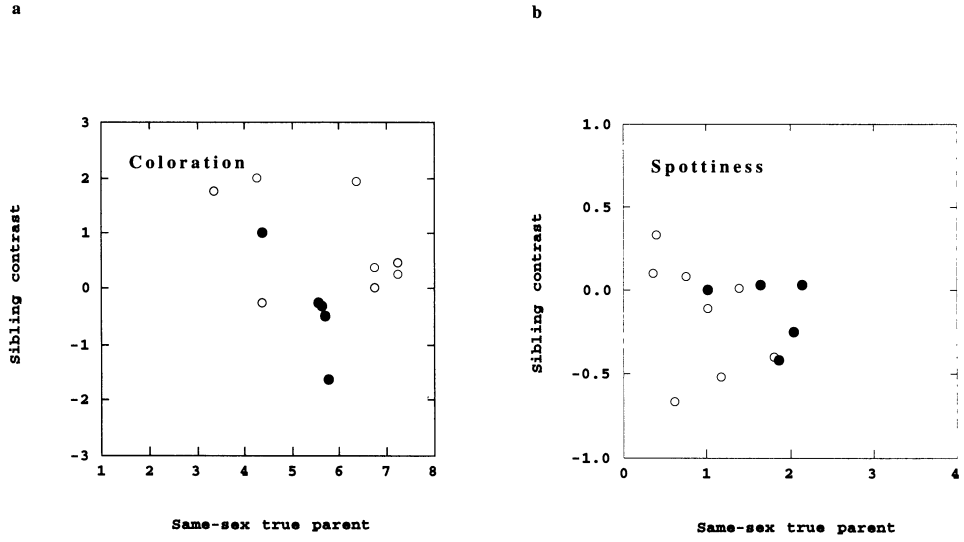

FIG. 6. Difference (contrast) in plumage coloration (a), and spottiness (b), of same-sex siblings raised in enlarged versus reduced broods in relation to the trait value of the same-sex true parent. Positive contrasts indicate that nestlings in enlarged broods were lighter colored or spottier than their siblings in reduced broods. Open circles refer to males and closed circles to females.

shown in the collared flycatcher, *Ficedula albicollis*, where paternal investment is traded against sexiness: Males involved in the rearing of experimentally enlarged broods had a reduced forehead white patch the following year and males of reduced broods a larger one (Gustafsson et al. 1995).

Our results suggest that the rearing environment does not account for a large proportion of the observed variance in plumage coloration and spottiness. However, the findings that unrelated nestmates were not similarly ornamented and that the brood size manipulation did not affect the ornamentations have to be interpreted with caution. A Type II error cannot be excluded; also, a genotype-by-environment interaction via the cross-fostering experiment cannot be assessed reliably with small samples and was therefore omitted.

Genetic Effect on Ornamentation

We quantified ornamentation in nestlings rather than in recruits (e.g., Hill 1991; Møller 1991; Slagsvold and Lifjeld 1992; Norris 1993). Quantification of ornaments in recruits bears the problem that more ornamented birds may be more often recruited in the breeding population than less ornamented ones (Møller 1992), which may lead to inflated heritability estimates. This potential error is reduced if one can quantify ornaments already in nestlings, as in the present study. Because we showed that additive genetic variance is maintained for plumage coloration and spottiness, these traits can respond to phenotypic selection. Observations in Switzerland showed that female plumage spottiness was positively correlated with clutch size, that dark males had a higher reproductive success than whiter males, and that old females were mated with whiter yearling males than first-year females (unpubl. data). This suggests that dark males are better fathers, lightly coloured males have mating advantages, and that female plumage spottiness may signal egg productivity. This scenario may be interesting for understanding variation in plumage characteristics of this species. To this end, studies are required to determine if dark and light plumages or immaculate and heavily flecked plumages: (1) correspond to different genetically inherited ESS-breeding tactics (Maynard Smith 1982; Lank et al. 1995); (2) serve individual recognition (Whitfield 1988); or (3) signal genotypic quality (Møller 1990; Petrie 1994). A cost-benefit analysis of the various plumage patterns may be useful for understanding cline variation (Voous 1950; Møller 1995).

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LITERATURE CITED

ANDERSSON, M. 1982. Female choice selects for extreme tail length in a widowbird. Nature 299:818–820.

———. 1986. Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. Evolution 40:804–816.

BAKER, K. 1993. Pp. 276–280 *in* Identification guide to European non-passerines. BTO Guide 24. Tring, London.

BAUDVIN, H. 1975. Biologie de reproduction de la Chouette effraie (*Tyto alba*) en Côte d'Or: premiers résultats. Le Jean le Blanc 14:1–51.

———. 1978. Le cannibalisme chez l'Effraie *Tyto alba*. Nos Oiseaux 34:223–231.

BOAG, P. T., AND A. J. VAN NOORDWIJK. 1987. Quantitative genetics. Pp. 45–78 *in* F. Cooke and P. A. Buckley, eds. Avian genetics: a population and ecological approach. Academic Press, London.

CRAMP, S., AND K. E. L. SIMMONS. 1985. Handbook of the Birds of Europe, the Middle East and North Africa: the birds of the Western Paleartic. Vol. IV. Terns to Woodpeckers. Oxford Univ. Press, Oxford, U.K.

FALCONER, D. S. 1989. Introduction to quantitative genetics. 2d ed. Longman, New York.

FISHER, R. A. 1958. The genetical theory of natural selection. 2d ed. Dover, New York.
GRAY, D. A. 1996. Carotenoids and sexual dichromatism in North American passerine birds. Am. Nat. 148:453–480.
GUSTAFSSON, L., A. QVARNSTRÖM, AND B. C. SHELDON. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. Nature 375:311–313.
HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? Science 218:384–387.
HILL, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339.
———. 1992. Proximate basis of variation in carotenoid pigmentation in male house finches. Auk 109:1–12.
———. 1994. Geographic variation in male ornamentation and female mate preference in the house finch: a comparative test of models of sexual selection. Behav. Ecol. 5:64–73.
HILL, G. E., AND R. MONTGOMERIE. 1994. Plumage colour signals nutritional condition in the house finch. Proc. R. Soc. Lond. B 258:47–52.
HOELZER, G. A. 1989. The good parent process of sexual selection. Anim. Behav. 38:1067–1078.
KODRIC-BROWN, A., AND J. H. BROWN. 1984. Truth in advertising: the kinds of traits favored by sexual selection. Am. Nat. 124: 309–323.
LANDE, R. 1987. Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. Pp. 83–94 *in* J. W. Bradbury and M. B. Andersson, eds. Sexual selection: testing the alternatives. Wiley, Chichester, U.K.
LANK, D. B., C. M. SMITH, O. HANOTTE, T. BURKE, AND F. COOKE. 1995. Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. Nature 378:59–62.
MAYNARD SMITH, J. 1982. Evolution and the theory of games. Cambridge Univ. Press, Cambridge, U.K.
MØLLER, A. P. 1988. Female choice selects for male sexual tail ornaments in the monogamous swallow. Nature 332:640–642.
———. 1989. Viability costs of male tail ornaments in a swallow. Nature 339:132–135.
———. 1990. Effects of a haematophagous mite on the barn swallow (*Hirundo rustica*): a test of the Hamilton and Zuk hypothesis. Evolution 44:771–784.
———. 1991. Sexual selection in the monogamous barn swallow (*Hirundo rustica*). I. Determinants of tail ornament size. Evolution 45:1823–1836.
———. 1992. Sexual selection in the monogamous barn swallow (*Hirundo rustica*). II. Mechanisms of sexual selection. J. Evol. Biol. 5:603–624.
———. 1995. Sexual selection in the barn swallow (*Hirundo rustica*). V. Geographic variation in ornament size. J. Evol. Biol. 8:3–19.
MØLLER, A. P., AND F. DE LOPE. 1994. Differential costs of a secondary sexual character: an experimental test of the handicap principle. Evolution 48:1676–1683.
NORRIS, K. 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. Nature 362:537–539.
PETRIE, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. Nature 371:598–599.
RICHNER, H. 1989. Avian laparoscopy as a field technique for sexing birds and an assessement of its effects on wild birds. J. Field Ornithol. 60:137–142.
ROHWER, S., AND F. C. ROHWER. 1978. Status signalling in Harris sparrows: experimental deceptions achieved. Anim. Behav. 26: 1012–1022.
ROULIN, A. 1996a. Dimorphisme sexuel dans la coloration du plumage chez la Chouette effraie (*Tyto alba*). Nos Oiseaux 43:517–526.
———. 1996b. Balz und Paarbildungserfolg bei der Schleiereule *Tyto alba*. Orn. Beob. 93:184–189.
SCHÖNFELD, M., AND G. GIRBIG. 1975. Beiträge zur Brutbiologie der Schleiereule, *Tyto alba*, unter besonderer Berücksichtigung der Abhängigkeit von der Feldmausdichte. Hercynia 12:257–319.
SLAGSVOLD, T., AND J. T. LIFJELD. 1985. Variation in plumage colour of the great tit *Parus major* in relation to habitat, season and food. J. Zool. Lond. (A) 206:321–328.
———. 1992. Plumage color is a condition-dependent sexual trait in male pied flycatchers. Evolution 46:825–828.
SWADDLE, J. P., AND M. S. WITTER. 1994. Food, feathers and fluctuating asymmetries. Proc. R. Soc. Lond. B 255:147–152.
TAYLOR, I. R. 1993. Age and sex determination of barn owls *Tyto alba alba*. Ring. Migr. 14:94–102.
———. 1994. Barn owls: predator-prey relationships and conservation. Cambridge Univ. Press, Cambridge, U.K.
VOOUS, K. H. 1950. On the distributional and genetical origin of the intermediate populations of the Barn Owl (*Tyto alba*) in Europe. Pp. 429–443 *in* Geest and K.-G. Portig, eds. Syllegomena biologica. Verlag, Leipzig, Germany.
WHITFIELD, D. P. 1988. The social significance of plumage variability in wintering turnstone *Arenaria interpres*. Anim. Behav. 36:408–415.
WILKINSON, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL.
WILSON, R. T., M. P. WILSON, AND J. W. DURKIN. 1986. Growth of nestling barn owls *Tyto alba* in central Mali. Ibis 129:305–318.
ZAHAVI, A. 1975. Mate selection—a selection for a handicap. J. Theor. Biol. 53:205–214.

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