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A female melanin ornament signals offspring fluctuating asymmetry in the barn owl

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Sexual selection theory predicts that males advertise quality by displaying extravagant ornaments. By contrast, whether phenotypic variation in females has a signalling function remains an open question. Here, to our knowledge, we provide the first evidence that a female plumage trait can signal fluctuating asymmetry in the offspring. We experimentally demonstrate in wild barn owls (*Tyto alba*) that the extent to which females display black spots on their plumage does not only signal offspring parasite resistance as shown in a previous study but also developmental homeostasis in the offspring. A greater number of spotted females produced offspring that had more symmetrical feathers during the period of growth. Males, that pair non-randomly with respect to female plumage spottiness therefore appear to gain substantial benefits by mating with heavily spotted females. Genetic variation in plumage spottiness is nevertheless maintained as the covariation between offspring body mass and mother plumage spottiness varies annually depending on environmental conditions.

Keywords: balanced selection; developmental homeostasis; female ornament; fluctuating asymmetry; genetic variation; *Tyto alba*

1. INTRODUCTION

In many animal species the display of an ornament attractive to choosy females provides mating advantages leading to the evolution of extravagant traits in males (Andersson 1994). Although females frequently vary in phenotypic traits little is known of the adaptive value of this variation (Amundsen 2000), as it generally appeared that a phenotypic trait signals quality when expressed in males rather than in females (Muma & Weatherhead 1989; Hill 1993; Cuervo *et al.* 1996). However, all these studies focused on phenotypic traits that are expressed to a larger extent in males. Because males pass on genes coding for such traits to their daughters, as well as sons, females are indeed expected to express male-specific traits even if only males are under selection to signal quality with such displays (Cuervo *et al.* 1996). To circumvent this problem, investigating whether females advertise quality with a phenotypic trait should be approached through the study of traits that are more conspicuously expressed in females than in males (Roulin *et al.* 2001*a*).

In the barn owl (*Tyto alba*), individuals vary in spottiness with plumage ranging from immaculate through to heavily marked with black spots. This trait is heritable, its expression is subject to neither the environment where individuals live nor their body condition (Roulin *et al.* 1998) and it does not covary with body size (Roulin 1999), indicating that differently spotted individuals may signal different attributes that have similar fitness values (Lank *et al.* 1995; Losey *et al.* 1997). Males are on average 1.9 times less spotted and female plumage spottiness is a criterion in mate choice (Roulin 1999). Experiments showed that more heavily spotted females produce offspring of both sexes that are better able to mount a humoral immune response against an artificially administrated antigen (Roulin *et al.* 2000) and are more resistant to ectoparasites (Roulin *et al.* 2001*b*). These results, found in four different years, support the Hamilton & Zuk (1982) hypothesis that parasites play a part in the evolution of plumage traits such as spottiness, even in females. However, it is still possible that this female trait has a broader signalling function.

To investigate this hypothesis, we performed two studies where we measured developmental stability in relation to plumage spottiness with the prediction that offspring of more heavily spotted mothers are developmentally more stable. Developmental processes can be disturbed by a variety of genetic and environmental stress factors occurring during growth. As an index of developmental stability, we consider bilateral symmetry of wing feathers (so called fluctuating asymmetry (FA)). FA is the macroscopic expression of microscopic errors in the biosynthesis of two sides of the body that are supposed to be under the control of the same genes and environment (Møller & Swaddle 1997). In the first study performed in Switzerland in 2001, we randomly allocated hatchling barn owls in 44 foster nests to ensure that any relationship between

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mother plumage spottiness and FA measured in the offspring is not due to environmental factors experienced during growth but to parental characteristics (genotypic or pre-hatching maternal effects). Plumage spottiness was measured in the adults and FA in the length of primary feathers in the cross-fostered offspring. In the second study, we measured asymmetry in wing feathers of male and female barn owls collected dead along French roads. If offspring of more heavily spotted are not only more immunocompetent against an artificially administrated antigen (Roulin *et al.* 2000) and more resistant against ectoparasites (Roulin *et al.* 2001*b*) but also developmentally more stable, a lightly spotted plumage should signal another quality if genetic variation in plumage spottiness is at stake. To investigate this issue, we examined offspring body condition in relation to female plumage spottiness from 1994 to 2001.

2. METHOD

(a) *The model organism and the assessment of plumage spottiness*

In the study area, barn owls lay 2–11 eggs (the mean is six eggs) from 5 March to 30 July (the mean laying date is 30 April; Roulin 2002*a*). Females incubate the eggs, which take 32 days to hatch. Offspring hatch asynchronously, *ca.* 2–3 days apart. Brood reduction is frequent in the first three weeks and nestlings spend two months in the nest before fledging. Sex-roles in reproduction are well defined with the mother brooding the young and distributing small mammals brought by her partner. When the young are three weeks of age, the mother provides one-third of the food. In Switzerland, half of the double-brooded females desert their offspring half way through the rearing period to remate with another partner (see the review in Roulin 2002*b*). Although females are 6% heavier than males, there was no sexual dimorphism in wing length among 184 and 226 different Swiss breeding males and females (student *t*-test: $t_{408} = 0.54$, $p = 0.59$; 296.7 ± 0.3 mm; A. Roulin, unpublished data). In the young, asymptotic wing length is achieved at 70 days of age, that is about two weeks after the first flight at around 55 days (Taylor 1994).

Barn owls display black spots on the body underparts. Each feather can have one to four spots. A.R. assessed the amount of spots on the breast, belly, flanks and underside of the wings by using a 60 mm × 40 mm frame. Between 0 and 139 spots were counted, and with a calliper the diameter of 1 to 26 most representative spots were measured to the nearest 0.1 mm (diameters range from 0.3 to 4.5 mm). For each body part, we then calculated the percentage of the surface covered by spots using the formula $100 \times \pi \times$ number of dots $\times$ (mean spot diameter/2)^2/(60 × 40), a value that can range from 0 to 19%. This value was square-root transformed for normality, and values found on the two flanks were averaged as well as those found on the two wings. The mean value of the four body parts was referred to as 'plumage spottiness' and used in the statistical analyses.

(b) *Feather asymmetry among cross-fostered offspring*

One to three hatchlings (the mean brood size is 4.5 and mean number of cross-fostered chicks is 1.9) were exchanged among pairs of nests. After transfer, rank 1 was assigned to the oldest chick of the brood, rank 2 to the second oldest chick, and so on. The mean rank of cross-fostered offspring was not significantly correlated with plumage spottiness of their genetic mother and father (Spearman rank correlation: $p > 0.11$). Therefore, if chicks in poorer condition (Roulin 1998) display higher FA, the place in the within-brood age hierarchy was not a confounding variable of the covariation between FA and mother plumage spottiness. Hatching date of the older offspring was not correlated with mother and father plumage spottiness (Pearson correlation: $p > 0.58$). Sex of the nestlings was determined with the molecular techniques gene method (Roulin *et al.* 1999). Without pulling out wing feathers it is impossible to measure feather length precisely in living birds. To circumvent this problem, on 40- to 59-day-old chicks (the mean is 50 days) two adjacent feathers were laid on top of one another and the distance from tip to tip was measured. Feathers were not fully grown and the shafts were clear when measured (because the shafts of tail feathers were not clear, we did not measure asymmetry of this trait). For example, if P10 (i.e. the 10th primary feather) measured 224 mm and P9 measured 233 mm, the difference (Δ1) between the two tips was 9 mm. Using a calliper, A.R. measured to the nearest 0.1 mm the Δ1 between P10 and P9, between P9 and P8 (Δ2), P8 and P7 (Δ3), P7 and P6 (Δ4), P6 and P5 (Δ5), P5 and P4 (Δ6), P4 and P3 (Δ7), P3 and P2 (Δ8), and between P2 and P1 (Δ9). Then for each difference (e.g. Δ1), measured four times on the same day and then averaged, we subtracted the mean value found in the right wing from the mean value found in the left wing ($\Delta 1_{right} - \Delta 1_{left}$). This was done for the nine differences Δ1 to Δ9, and then we summed these nine unsigned values (mean ± s.e unsigned FA is 7.4 ± 0.2 mm). This composite absolute value was log transformed to normalize the data. Our method of measuring FA overestimates the degree of true FA because if one feather is asymmetrical, then this will influence the difference in feather lengths between the two sides for two pairs of feathers. This is, however, not a problem in our study, because we are interested in the covariation between FA and a plumage trait. Such a covariation should be the same if assessed with true FA or with a measure that is strongly correlated to FA. Indeed, FA measured following our method provided a reliable estimate of true FA in the length of wing feathers as demonstrated with 93 dead owls. In the latter birds, the correlation between the composite index of FA (true FA, see below) and FA estimated via the method developed here was significant ($r = 0.80$, $n = 93$, $p < 0.001$). As mentioned above, the differences Δ1 to Δ9 were measured four times allowing us to estimate the repeatability of FA assessment (one-way ANOVA: $F_{79,240} = 12.24$, $p < 0.001$; repeatability ± 1 s.e. = 0.74 ± 0.04). To avoid pseudoreplication, we calculated a mean sibling value so that each mother is only represented once in each analysis. Note that FA was not significantly correlated with mean number of ectoparasites *Carnus hemapterus* per nestling measured when the oldest young was 28 days of age ($r = 0.13$, $n = 42$ nests, $p = 0.42$). Wing length of the growing offspring (i.e. 202 to 248 mm; mean of 230 mm) at the time of FA measurement was not significantly correlated with plumage spottiness of genetic parents ($p > 0.20$) and FA ($r = 0.16$, $n = 43$, $p = 0.31$) indicating that the degree of development was not a confounding factor.

To test properties of our FA measurements, we calculated the nine signed differences (e.g. $\Delta 1_{right} - \Delta 1_{left}$), summed them and calculated a mean sibling value. Sums were normally distributed (Lilliefors' test: $p = 0.13$) and significantly different from zero (paired *t*-test: $t_{42} = 2.79$, $p = 0.008$; skewness: 0.44, kurtosis: 0.10). Larger differences were measured on the right than left wings indicating systematic measurement errors. Because plu-

mage spottiness of genetic mothers was not significantly correlated with mean coefficient of variation calculated over the four measurements of FA of their foster offspring ($r = 0.12$, $n = 43$, $p = 0.46$), measurement errors did not blur the relationship between FA and mother plumage spottiness.

(c) *Feather asymmetry among adults*

From 17 January 2000 to 4 April 2001, 93 dead barn owls were collected in the regions of Champagne and Lorraine, France. Owls stayed less than a day along the roads before being collected. Birds in which we found the immune organ bursa of Fabricius belonged to the age class 'juvenile' ($n = 74$ individuals). Those in which this organ was missing and for which primary and secondary feathers all belonged to the same new generation, were classified as 'yearlings' ($n = 10$). In the case where wing feathers were not of the same generation, birds were referred to as 'adults' ($n = 9$). A.R. pulled out 10 primary feathers (P10 to P1) and 11 secondary feathers (S1 to S11) from each wing (in addition to pulling feathers and measuring them, they were first measured in the same manner as was done on the nestlings). Blindly with respect to bird identity, feathers of one wing (right or left, chosen randomly) were measured to the nearest millimetre before measuring those of the other wing. For each single pair of feathers (e.g. P1 of the right and left wings), we calculated their unsigned difference in lengths and then summed values found in the 21 pairs of feathers. (Note that in eight cases one feather was broken, missing or growing; in three cases, two feathers; and in one case, four feathers; these birds were excluded from the statistical analyses.) This later value provided a composite index of FA in feather length (mean unsigned FA is 12.7 ± 4.2 mm; range of 6–26 mm). To test whether this index is reliable, F.B. remeasured all feathers two months later. Composite indices determined by both observers were significantly repeatable ($F_{92,93} = 8.53$, $p < 0.001$; repeatability ± 1 s.e. $= 0.79 \pm 0.04$). For each individual, we averaged composite indices of both observers and log transformed this value for normalization. We used this later value in statistical analyses. FA was not correlated with mean feather length ($r = 0.05$, $n = 93$, $p = 0.66$). There was also no significant correlation between FA and the size of the bursa of Fabricius given by the product of length by width measured to the nearest 0.1 mm using a calliper ($r = -0.19$, $n = 72$, $p = 0.11$; it was destroyed in two individuals). Among juveniles this mean index was not correlated with the interval in days between the date of cadaver collection and 1 June (arbitrary reference for birth date; $r = -0.11$, $n = 74$, $p = 0.33$). This indicates that inter-individual variation in FA was not due to inter-individual variation in feather wear. To further investigate whether there might be some significant feather wear, we tested whether wing length decreases within breeding individuals between the first and second year of age (A. Roulin, unpublished data from the Swiss population). We considered these two age classes because birds start to moult their wing feathers in their second year (see the review in Roulin 2002*b*). The finding that wing length did not decrease between the first and second year of age (ANOVA with wing length as the dependent variable and controlling for bird identity; effect of age: $F_{1,93} = 0.18$, $p = 0.67$) indicates that feather wear is negligible.

To test properties of our composite indices of FA, for each pair of feathers (e.g. P1) we calculated the signed length difference between feathers of the right and left wings. For each individual, we then summed the signed differences found in the 21 pairs of feathers. This measure is reliable, as it was significantly repeatable among observers (repeatability ± 1 s.e.: 0.91 ± 0.02; $F_{92,93} = 20.24$, $p < 0.001$). These signed summed values were normally distributed (Lilliefors' test: $p = 0.45$) but slightly centred above zero (2.00 mm; range of -15.5 to 15.0 mm; paired *t*-test comparing signed summed values with zero: $t_{92} = 3.15$, $p = 0.002$; skewness: -0.22; kurtosis: 0.33), indicating systematic measurement errors. Note however, that mean length of feathers from the right wing was not significantly different from mean length of feathers from the left wing ($t_{92} = 1.59$, $p = 0.12$).

(d) *Nestling body condition in relation to mother plumage spottiness*

For two reasons, we measured body mass and wing length only in nestlings aged between 11 and 36 days. First, rearing condition affects body mass in this period but not at fledging (Durant & Handrich 1998; Roulin 1998). Second, in this period the relationship between log-transformed body mass and log-transformed wing length is linear (A. Roulin, unpublished data); log transformation was necessary to get a linear relationship. In total, we have a sample of 1395 nestlings that successfully fledged from 359 broods between 1994 and 2001. We extracted residuals from an ANOVA with log body mass as the dependent variable, log wing length ($F_{1,1372} = 6580.97$, $p < 0.001$), hour of the day when nestlings had been measured ($F_{1,1372} = 119.14$, $p < 0.001$) and year ($F_{7,1372} = 3.42$, $p = 0.001$) as independent variables. These residuals provide an index for body condition independently of age, because food supply affects body mass but not wing length (Durant & Handrich 1998; Roulin 1998). For each nest, we considered the residual value of the last-hatched nestling but not of the other nest-mates because brood size manipulation experiments affected body condition of the former nestlings only (Roulin 1998). For each of the 8 years, we introduced in an ANOVA the body condition index of the youngest nestling as the dependent variable, female plumage spottiness, hatching date and brood size as independent variables, and we extracted the β-standardized effect of female plumage spottiness.

(e) *Statistics*

All statistical analyses are two-tailed and *p*-values smaller or equal to 0.05 considered as significant.

3. RESULTS AND DISCUSSION

As expected, FA of cross-fostered offspring was smaller when the genetic mother was more heavily spotted (figure 1; partial correlation; effect of genetic mother after controlling for spottiness of foster mother: $r_{part} = -0.32$, $n = 43$, $p = 0.038$; foster mother after controlling for spottiness of genetic mother: $r_{part} = -0.09$, $n = 43$, $p = 0.59$). A similar relationship between FA of cross-fostered offspring and plumage spottiness of genetic and foster fathers did not hold (genetic father after controlling for spottiness of foster father: $r_{part} = -0.11$, $n = 35$, $p = 0.52$; foster father after controlling for spottiness of genetic father: $r_{part} = -0.02$, $n = 35$, $p = 0.91$). Note that FA measured in the offspring was correlated with plumage spottiness of their genetic mother but not with their own spottiness (ANCOVA with mean FA of same-sex offspring as the dependent variable, plumage spottiness of genetic mother as a first covariate: $F_{1,56} = 4.96$, $p = 0.03$; mean plumage spottiness of same-sex offspring as a second covariate:

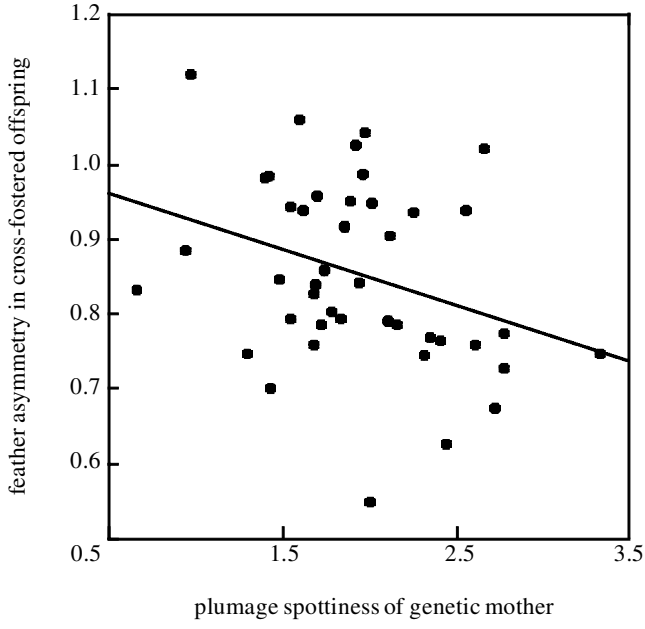

Figure 1. Asymmetry (log transformed) in feather length of cross-fostered offspring in relation to plumage spottiness of their genetic mother. The regression line is presented.

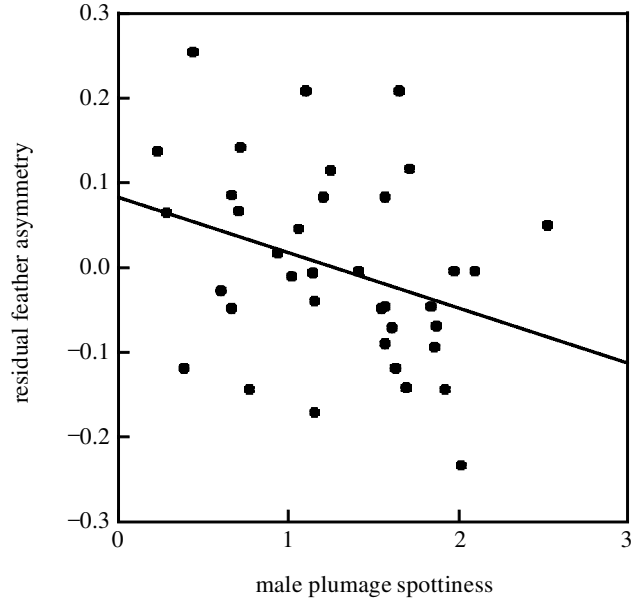

Figure 2. Relationship between residual feather asymmetry and plumage spottiness in males. Residuals were extracted from an ANOVA where the dependent variable was the log-transformed unsigned feather length asymmetry and the independent variable age. The Pearson correlation is $r = -0.33$, $n = 37$, $p = 0.046$. The regression line is presented.

$F_{1,56} = 0.04$, $p = 0.84$; sex of the offspring: $F_{1,56} = 0.05$, $p = 0.83$). Based on the fact that sons, in contrast to daughters, resemble their mother with respect to plumage spottiness (Roulin *et al.* 2001*a*), suggesting sex-linked inheritance (i.e. genes creating variation in spottiness may be located on the Z sex chromosome; in birds females are heterogametic), more spotted nestling males should be more symmetric, whereas no such relationship should be detected among nestling females. This was the case (Pearson correlation: $r = -0.43$, $n = 44$, $p = 0.004$ versus $r = -0.04$, $n = 43$, $p = 0.80$). Even if FA measured in growing individuals is not correlated with FA when fully grown, our results nevertheless indicate that female plumage spottiness reflects some aspect of developmental homeostasis in their offspring.

To examine whether the results of our experiment may be valid in fully grown individuals, we predicted that in a population more heavily spotted males display lower levels of FA not because they are themselves heavily spotted but because their mother was (prediction based on the fact that genes creating variation in spottiness may be located on the Z sex chromosome). To test this prediction, we measured asymmetry in wing feathers of barn owls collected dead along French roads. As expected, more heavily spotted males had significantly more symmetric wing feathers (figure 2; ANOVA: $F_{1,33} = 4.14$, $p = 0.05$). In this test, we statistically controlled for age ($F_{2,33} = 3.29$, $p = 0.05$; birds older than 1 year were more asymmetric). By contrast, and as predicted if the level of FA of an individual depends on plumage spottiness of its mother but not of itself, plumage spottiness in females was not significantly correlated with their level of FA (plumage spottiness: $F_{1,37} = 0.001$, $p = 0.97$; age: $F_{2,37} = 6.14$, $p = 0.005$).

How can genetic variation in plumage spottiness be maintained if heavily spotted mothers produce offspring that are better in a wide range of properties? A plausible mechanism is balancing selection (Losey *et al.* 1997)

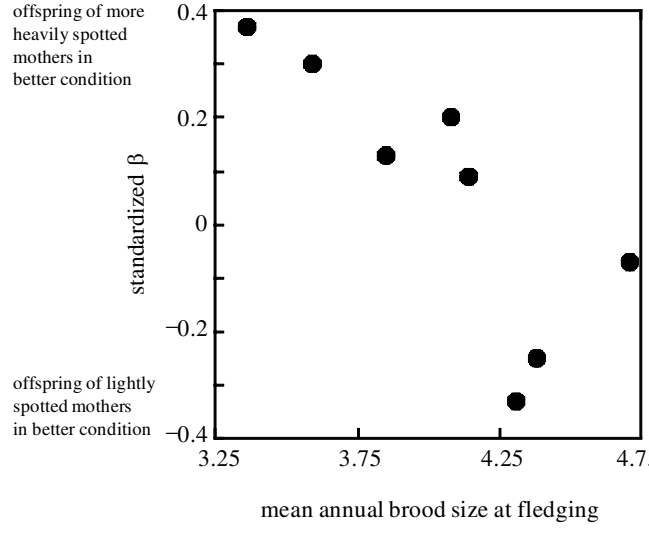

Figure 3. Relationship between female plumage spottiness and body condition of the younger offspring (standardized β calculated for each year from 1994 to 2001) in relation to mean annual brood size. Negative β-values indicate that the offspring of lightly spotted females were in better condition than those of more heavily spotted females, vice versa for positive β-values.

where variation in environmental quality determines the magnitude of the advantage of being heavily spotted. In some circumstances being less spotted may be beneficial, so that heavily and lightly spotted females achieve a similar fitness. We tested this hypothesis by using a dataset on offspring body condition (residuals from the regression of offspring body mass on offspring wing length) collected from 1994 to 2001 in Switzerland. For each of the 8 years, we determined the extent to which more heavily spotted females produced offspring in better condition (β-values).

We then correlated these eight β-values with mean annual brood size in order to detect whether the benefit of a particular plumage pattern is correlated with some environmental factors that vary from one year to the next. We found a strong negative relationship (figure 3; Spearman rank correlation: $r_s = -0.88$, $n = 8$, $p = 0.004$; over the 8 years mean β is 0.05 and hence, on average, offspring condition is independent of mother plumage spottiness). This indicates that in years when broods were larger, lightly spotted females produced offspring that were in better condition than the ones of heavily spotted females. This indicates that heavily spotted females have an advantage by producing offspring that show better developmental homeostasis and are more resistant to parasites (Roulin *et al.* 2000, 2001*b*), whereas lightly spotted females benefit from some other unknown advantage when rearing conditions are apparently good.

The discovery that a female plumage trait can signal several qualities in the offspring demonstrates that investigation of the good gene theory of sexual selection (Hamilton & Zuk 1982; Andersson 1994) should not only focus on male traits. It might well be that in many organisms, including humans (Zaadstra *et al.* 1993), females advertise quality by displaying female-specific traits. Because offspring share half of their genome with their mother, there is no *a priori* reason to believe that only males pass on good genes to their progeny. Maternal transfer of good gene products into eggs (Gil *et al.* 1999) may also further increase the potential for females to advertise quality.

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REFERENCES

Amundsen, T. 2000 Why are female birds ornamented? *Trends Ecol. Evol.* **15**, 149–155.

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Cuervo, J. J., de Lope, F. & Møller, A. P. 1996 The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behav. Ecol.* **7**, 132–136.

Durant, J. M. & Handrich, Y. 1998 Growth and food requirement flexibility in captive nestlings of the European barn owl (*Tyto alba*). *J. Zool. Lond.* **245**, 137–145.

Gil, D., Graves, J., Hazon, N. & Wells, A. 1999 Male attractiveness and differential testosterone investment in zebra finch eggs. *Science* **286**, 126–128.

Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

Hill, G. E. 1993 Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution* **47**, 1515–1525.

Lank, B. L., Smith, C. M., Hanotte, O., Burke, T. & Cooke, F. 1995 Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. *Nature* **378**, 59–62.

Losey, J. E., Ives, A. R., Harmon, J., Ballantyne, F. & Brown, C. 1997 A polymorphism maintained by opposite patterns of parasitism and predation. *Nature* **388**, 269–272.

Møller, A. P. & Swaddle, J. P. 1997 *Asymmetry, developmental stability, and evolution*. Oxford University Press.

Muma, K. E. & Weatherhead, P. J. 1989 Male traits expressed in females: direct or indirect sexual selection? *Behav. Ecol. Sociobiol.* **25**, 23–31.

Roulin, A. 1998 Importance de la nichée et croissance pondérale chez les jeunes chouettes effraies *Tyto alba*. *Alauda* **66**, 273–278.

Roulin, A. 1999 Non-random pairing by male barn owls *Tyto alba* with respect to a female plumage trait. *Behav. Ecol.* **10**, 688–695.

Roulin, A. 2002*a* Short- and long-term fitness correlates of rearing conditions in barn owls. *Ardea* **90**, 259–267.

Roulin, A. 2002*b* *Barn owl. Update of the birds of the western Palearctic*. Oxford University Press.

Roulin, A., Richner, H. & Ducrest, A.-L. 1998 Genetic, environmental and condition-dependent effects on female and male ornamentation in the barn owl *Tyto alba*. *Evolution* **52**, 1451–1460.

Roulin, A., Ducrest, A.-L. & Dijkstra, C. 1999 Effect of brood size manipulations on parents and offspring in the barn owl, *Tyto alba*. *Ardea* **87**, 91–100.

Roulin, A., Jungi, T. W., Pfister, H. & Dijkstra, C. 2000 Female barn owls (*Tyto alba*) advertise good genes. *Proc. R. Soc. Lond.* B **267**, 937–941. (DOI 10.1098/rspb.2000.1093.)

Roulin, A., Dijkstra, C., Riols, C. & Ducrest, A.-L. 2001*a* Female- and male-specific signals of quality in the barn owl. *J. Evol. Biol.* **14**, 255–266.

Roulin, A., Riols, C., Dijkstra, C. & Ducrest, A.-L. 2001*b* Female plumage spottiness and parasite resistance in the barn owl (*Tyto alba*). *Behav. Ecol.* **12**, 103–110.

Taylor, I. R. 1994 *Barn owls: predator–prey relationships*. Cambridge University Press.

Zaadstra, B. M., Seidell, J. C., Van Noord, P. A. H., Egbert, R., Habbema, J. D. F., Vrieswijk, B. & Karbaat, J. 1993 Fat distribution and female fecundity: prospective study of effect of body fat distribution on conception rates. *Br. Med. J.* **306**, 484–487.