Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait

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In socially monogamous species it is rare for females to be more intensely colored than males. The barn owl (*Tyto alba*) is one of the exceptions, as females usually exhibit more and larger black spots on the plumage. The evolution of sexual dimorphism in plumage traits is commonly assumed to be the result of sexual selection. I therefore examined the prediction that male barn owls do not pair randomly with respect to female plumage spottiness during a 5-year study in Switzerland. The prediction was supported, as males that changed mates acquired a new female that was similarly spotted to the previous one, and pairing with respect to plumage spottiness was positively assortative. Significant repeatability in male pairing was presumably neither the consequence of sharing the same habitats with females displaying a given plumage spottiness nor of morphological characteristics of the males that could influence mate sampling. A resemblance in plumage spottiness between the mates of sons and of their father suggests that repeatability could have resulted from sexual imprinting and/or heritable variance in male preference for spotted females. To test whether males assess female plumage spottiness, I either cut off black spots or small pieces of feathers but not the spots of already mated females. Males mated to females with reduced plumage spottiness fed their brood at a lower cadency and achieved a lower reproductive success than other males. This experiment further suggests that female plumage spottiness is a stimulus for males. *Key words:* assortative mating, barn owls, male mate choice, phenotypic correlation, repeatability, sexual dimorphism, *Tyto alba.* [Behav Ecol 10:688–695 (1999)]

In species with conventional sex roles in reproduction, with females incubating the eggs and being strongly involved in the rearing of the young, females are usually not ornamented or express a similar, but less extravagant, ornamentation to males (Trivers, 1972). The evolution or maintenance of female ornamentation proceeds from direct or indirect sexual selection processes (Lande, 1980). The direct selection hypothesis posits that males and females benefit from displaying an ornament. Sexual dimorphism would therefore be maintained when the intensity of sexual selection on the sex trait is stronger on males or when natural selection against the expression of the trait is more intense in females (Burley, 1977; Martin and Badyaev, 1996; Trivers, 1972). The indirect selection hypothesis argues that the degree of expression of a male ornament in females is of no fitness value. The trait is expressed in females because it is sexually selected in males and genetically correlated between the sexes (Lande, 1980).

Several empirical studies concluded that in birds the expression of a male trait in females is the mere consequence of a genetic correlation between the sexes (Cuervo et al., 1996; Hill, 1993; Muma and Weatherhead, 1989; but see Tella et al., 1997), whereas other authors proposed that a male ornament expressed in females is used by males to choose a mate (Amundsen et al., 1997; Hill, 1993; Jones and Hunter, 1993; Møller, 1993), perhaps because the trait honestly signals female quality (Amundsen et al., 1997; Johnsen et al., 1996; Møller, 1993; Potti and Merino, 1996). However, Halliday and Arnold (1987) and Hill (1993) stressed the possibility that females may be selected to choose ornamented males and that females will produce choosy sons if the preference is heritable and genetically correlated between the sexes. In that case, male mate choice can be observed but may not be under direct selection.

In species where females are more ornamented than males, the greater expression of a plumage trait in females may have evolved through male mate choice for females displaying the trait to a greater degree. Most of these species usually have a polyandrous mating system where the roles in reproduction are reversed, with males incubating the eggs and being strongly involved in parental care (Emlen and Oring, 1977). The barn owl (*Tyto alba*) may be an exception, as it is socially monogamous and commonly females display more and larger black spots on the plumage of the ventral body side than males (Roulin, 1999; present study). To evaluate the hypothesis that males pair nonrandomly with respect to female plumage spottiness, I used observational data, and to test whether males assess female plumage spottiness I designed an experiment, as described below.

Over a period of 5 years, I studied breeding pairs in Switzerland. I examined the prediction of nonrandom male pairing, which argues that males changing mates between two breeding attempts acquire a new female that is similarly spotted to the first one, or, in other words, that male pairing with respect to female plumage spottiness is repeatable (Lessells and Boag, 1987). To my knowledge, after Møller's study (1994a) on barn swallows (*Hirundo rustica*), the present work is the second reporting repeatability of pairing pattern in the field, and the first reporting repeatability of male pairing pattern.

In the experimental portion of the study, I manipulated female plumage spottiness after pair formation and then mea-

sured parental feeding rates and reproductive success. If female plumage spottiness is a stimulus for males, I predicted that males would reduce their investment in reproduction after black spots are removed from the plumage of their mates. Consequently, the feeding rate of males and their reproductive success are expected to decrease when female plumage spottiness is experimentally reduced. Such a behavioral change may be due to the fact that they do no more recognize their mate (e.g., Whitfield, 1986) or that investment in reproduction by males is positively related to the expression of the mate's plumage spottiness (e.g., de Lope and Møller, 1993; Møller, 1994b).

METHODS

The barn owl

The barn owl is a noncolonial, medium-sized nocturnal raptor that breeds mainly in man-made cavities and dark places including nest-boxes. Population size varies markedly between years, mostly in relation to vole abundance and the severity of winters (Taylor, 1994). Adult owls are usually sedentary and start searching for a mate and nest site in winter (Roulin, 1998a). One or two clutches are produced per year consisting of 2–16 eggs each (mean: 5–6) (Taylor, 1994). Beside the variation in plumage spottiness, owls also vary in plumage coloration from dark-reddish brown to white, with males usually being lighter colored than females (Roulin, 1996, 1999). These traits are heritable, and their expression in nestlings was neither condition-dependent nor influenced by the rearing environment (Roulin et al., 1998). The subspecies *T. a. guttata,* which is characterized by reddish-brown plumage heavily marked with black spots, and *T. a. alba,* having white and less spotted plumage, originate from northeast Europe and the Mediterranean region, respectively, and interbreed in Switzerland (Voous, 1950).

Collection of observational data

Observational data were collected from 1994 to 1998 in an agricultural plain (range in altitude: 430–520 m above sea level; 46°49′ N, 06°56′ E). To locate breeding barn owls, 110 nest-boxes had been fastened to barns from 1987 onward. The number of clutches in my study population varied from year to year from 35 to 76. Breeding owls were captured in nest-boxes during incubation or the rearing of the young. As only females incubate the eggs and brood the young, they were recognized by the presence of a brood patch (Taylor, 1994). Age of the birds was known with precision when they had been ringed as nestlings, and only those birds have been considered in the analyses involving age. I estimated body size by measuring the lengths of the wings, central tail feathers, left tarsus, hind claws, and bill. All five measurements were taken on birds in 1997 and 1998 only, and I considered only birds from these 2 years when evaluating predictions based on body size. Relationships based on body mass were performed on 15 males and 28 females captured in the winters 1994–1995 to 1996–1997. The use of the winter body mass is justified by the fact that it varies to a lesser extent than mass during the breeding season (Taylor, 1994).

For every captured bird I quantified the extent of black pigments produced to form all black spots present on the ventral body side. On the breast, belly, flanks, and underside of the wings, I counted the number of spots within a 60×40 mm^2 frame. The diameter of 3–20 spots was measured to the nearest 0.1 mm with a calliper. For each body part, the formula $100\pi(\text{number of spots})[(\text{mean spot diameter}/2)^2]/2400$ was used to calculate the proportion of the 2400-mm^2 surface covered by black spots. I averaged the values of the two flanks, respectively, of the two wings, and then calculated the mean value from the four body parts. This last value was an index of overall plumage spottiness. Errors in the assessment of plumage spottiness are negligible, as two measures from same individuals taken 3–110 days apart were repeatable (repeatability ±SE, female: $r = 88\% \pm 2\%$, $F_{124, 125} = 14.7$, $p < .001$; male: $r = 96\% \pm 1\%$, $F_{30, 31} = 46.8$, $p < .001$).

To assess male plumage coloration on the same four body parts, I compared the coloration with eight color chips ranging from 1 for dark reddish-brown to 8 for white. The mean value from the four body regions provided an estimate of overall plumage coloration. Two measures taken on same individuals were highly correlated (female: $r_s = .95$, $p < .001$, $n = 125$; male: $r_s = .96$, $p < .001$, $n = 31$), and thus the method of assessing this plumage trait was reliable.

I measured the body mass of nestlings at all nests in 1996 when nestlings were on average 25 days old, in 1997 when they were on average 35 days old, and in 1998 at 40 days. For each brood a mean body mass was calculated from all nestlings. At 25 days of age the weight gain per day is maximal, whereas at 35 and 40 days the maximal body mass is reached. These values are more sensitive to environmental stress than body mass at fledging, which is achieved after body mass recession (Durant and Handrich, 1998; Roulin, 1998b).

Experimental data

Assessment of breeding parameters
The experiment was performed in 1997. In that year nest-boxes were regularly controlled to record clutch size and the number of hatchlings. The length and breath of each egg was measured with a caliper and volume (ml) was approximated with the formula length×breadth^2/1000. I approximated the age of nestlings by measuring wing length (Schönfeld and Girbig, 1975). I weighed nestlings when they were on average 35 days of age, and for each brood I calculated the mean value from all nestlings. Brood size at fledging is the number of 55-day-old nestlings.

Parental feeding rates were recorded during two successive nights when their offspring were on average 34 days of age (i.e., 1 month after the manipulation of plumage spottiness). I used an infrared sensitive camera and a VHS video camera to record entire nights (2130–0530 h). The camera was placed in nest-boxes or just beside the nest-box entrance one night before recording. Parents were captured at least 1 week before filming, and males and females were ringed on a different leg to recognize their sex on the video. The camera did not appear to disturb the owls. The measure "feeding rate" is the mean number of prey items brought to the nest per night. Twenty-eight out of the 33 nests used for the manipulation of female plumage spottiness were suitable for filming.

Manipulation of female plumage spottiness
When nestlings were on average 6 days of age I cut off most spots located on the tip of the feathers of 16 females (treatment "females with reduced plumage spottiness") and for 17 other females small pieces of the feathers but not the spots were cut off (treatment "females with spots"). I randomly assigned females to one of the two experimental treatments as they produced clutches of similar size (Mann-Whitney U test: $U = 116$, $p = .45$, $n = 16, 17$), eggs of similar volume ($t_{31} = -0.30$, $p = .77$), and their offspring hatched at a similar date ($t_{31} = -0.67$, $p = .51$). Their respective plumage spottiness did not significantly differ before manipulation (1.61 ± 0.56 versus 1.80 ± 0.67; $t_{31} = -0.92$, $p = .36$), whereas after the manipulation females with reduced plumage spottiness were
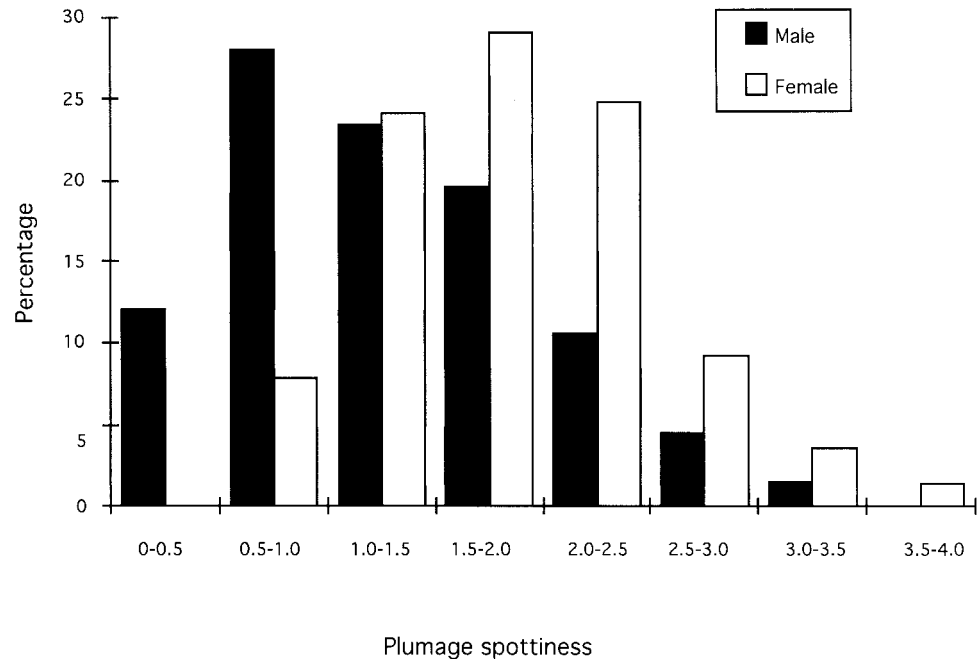
Figure 1
Distribution of the plumage spottiness of 132 breeding males and 141 breeding females captured from 1994 to 1998. The plumage spottiness of individuals captured in different years was averaged.

on average four times less spotted than females with spots (t_{31} = −8.05, $p < .001$). Females belonging to the two treatments were mated to males displaying similar plumage coloration (U = 134, $p = .94$, $n = 16, 17$). The manipulation of the feathers had no detectable harmful effects on females (Roulin, 1999).

Statistics

Statistical analyses were computed using the Systat statistical package (Wilkinson, 1989). Because plumage spottiness values did not always follow a normal distribution, I used the square root. Repeatabilities were computed according to Lessells and Boag (1987) and standard errors of repeatabilities according to Becker (1984). Unless stated, analyses were performed on individuals captured from 1994 to 1998. Tests are two-tailed and level of significance is .05. Means are reported ±1 SD.

RESULTS AND DISCUSSION

Variability of plumage spottiness

Breeding females were on average more spotted than males (1.83 ± 0.64, $n = 141$ versus 1.27 ± 0.69, $n = 132$; Student's t test: $t_{271} = 6.9$, $p < .001$; Figure 1). To assess whether plumage spottiness is an indicator of age, I compared mean plum-

age spottiness with mean age of individual birds (e.g., a breeding bird captured at the first and second year of life had a mean age of 1.5). This correlation was nonsignificant for males (Pearson correlation, $r = −.001$, $p = .99$, $n = 73$) and females ($r = .27$, $p = .08$, $n = 44$). Only one out of six measurements of body size was significantly correlated to female plumage spottiness (Table 1). In sum, plumage spottiness is sexually dimorphic, and probably neither a signal of age nor of body size.

Repeatability of male pairing with respect to female plumage spottiness

Based on 42 males that bred with 2–4 different females, successive different individual females of same males were similarly spotted (repeatability, $r = 29\% ± 11\%$, $F_{41, 68} = 2.1$, $p = .004$). This value is rather weak, perhaps because males had few pairing options. For instance, if between two breeding seasons most renesting females remained bonded to their mates (Roulin, 1998a), the pairing options of immigrants would be restricted. Between years, 42–60% of the renesting males changed mates, except between 1996 and 1997 when 18 out of 22 renesting males changed mates (82%, subsample of the above 42 males). Thus, males breeding in 1997 had theoretically all the same pairing options, and I predicted that re-

Table 1
Relationship between different measures of body size and plumage spottiness in male and female barn owls

	Male			Female		
	r	p	n	r	p	n
Length of wings	0.04	0.80	43	0.08	0.62	46
Length of central tail feathers	−0.04	0.82	43	0.42	0.004	46
Length of tarsus	−0.15	0.34	43	−0.04	0.81	46
Length of hind claw	−0.15	0.35	43	−0.13	0.81	46
Length of bill	0.16	0.32	43	−0.26	0.08	46
Winter body mass	−0.15	0.58	15	0.03	0.86	28

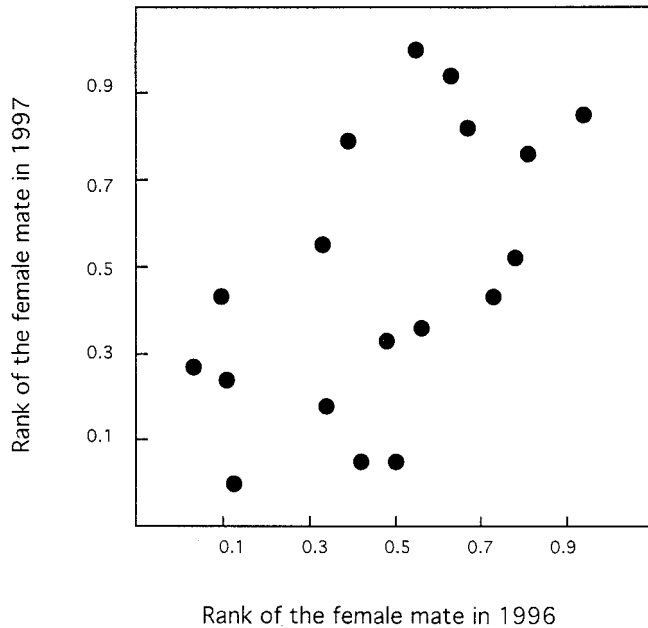Each bird appears only once in each analysis.

Figure 2
Relationship between the plumage spottiness of female mates of same males in 1996 and 1997. The rank 0 was assigned to the least and 1 to the most spotted female.

Figure 3
Relationship between the mean plumage spottiness of the father's and sons' mates.

peatability of male pairing with respect to female plumage spottiness would be larger than the 29% previously found. As expected, males that re-paired in 1997 mated with a female that was similarly spotted as the one they were paired with in 1996 ($r = 48\% \pm 18\%$, $F_{17, 18} = 2.8$, $p = .017$). Because of the turnover of the breeding population, available females in 1996 and 1997 were not all the same, and hence not similarly spotted.

To compare the relative plumage spottiness of two successive mates of the 18 males, I ranked females from the least (rank 0) to the most spotted individual (rank 1), and found a higher repeatability value ($r = 57\% \pm 16\%$, $F_{17, 18} = 3.6$, $p = .005$; Figure 2). This value is comparable with the ones found for female preference of male body coloration in two species of fishes (65%: Bakker, 1993; 58%: Godin and Dugatkin, 1995) and in the barn swallow for female preference of long-tailed males (57%) (Møller, 1994a). Repeatability of pairing determined under field conditions, as in the present study and in Møller's (1994) study, can be explained by at least three nonmutually exclusive hypotheses: (1) females are not randomly distributed among the habitats, (2) male morphological characteristics or experience (i.e., age) determine which male will pair with which kind of spotted females, and (3) there is a heritable or nonheritable variation in the magnitude of male preference (Jennions and Petrie, 1997).

Hypothesis 1: nonrandom distribution of birds among environments
The first hypothesis posits that a male repeatedly pairs to females displaying a given plumage spottiness because this male shares the same kind of habitats with those females. This hypothesis is, however, unlikely given that (1) in nest sites where different pairs bred (i.e., every individual bred in a nestsite with no more than one partner), successive females did not resemble each other in plumage spottiness ($r = -73\%$, $F_{47, 58} = 0.6$, $p = .96$), and (2) males that simultaneously changed mates and nest sites bred with a new female displaying plum-
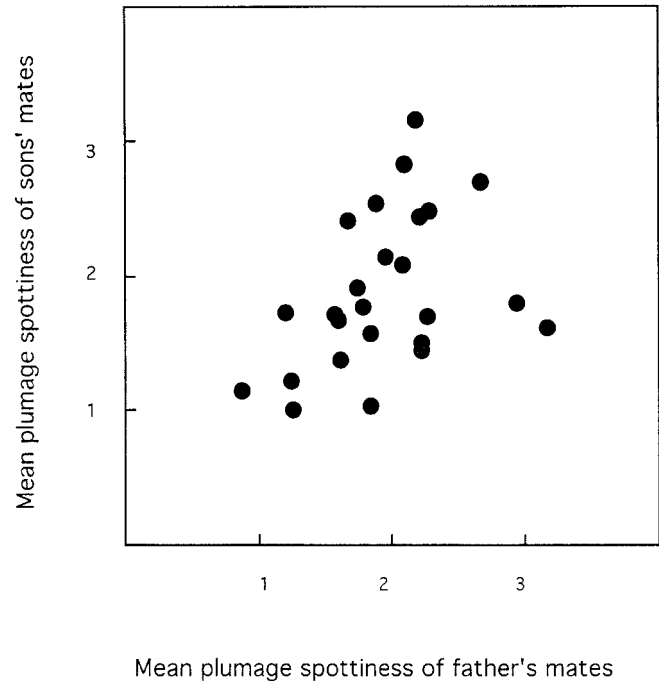
age spottiness to a similar extent as the previous one ($r = 45\% \pm 16\%$, $F_{20, 29} = 3.0$, $p = .004$). Assuming that the relative quality of nest sites does not vary over years, these two observations suggest that the repeatability of male pairing with respect to female plumage spottiness was not environmentally mediated.

Hypothesis 2: male morphological characteristics and experience
The second hypothesis proposes that males all have the same preference for heavily spotted females and their respective morphological characteristics or experience determine which kind of female a male obtains (Burley, 1977). This hypothesis predicts that there should be a close match between female plumage spottiness and some aspects of mate phenotype.

No significant correlation was found between metric measures of male body size and the mean plumage spottiness of their females (lengths of the wing, central tail feathers, bill, hind claw, tarsus; Pearson correlation: all r values between -0.24 and 0.08, all p values $>.10$, $n = 43$) and likewise for male winter body mass ($r = .01$, $p = .97$, $n = 15$) and male plumage coloration ($r = -.01$, $p = .92$, $n = 132$).

If experience is important in sampling females, older males should acquire spottier females than younger males. I assessed potential effects of male experience in acquiring the most spotted females in three ways. First, mean male age (e.g., when a male bred at 4 and 5 years, I used the mean male age 4.5) was not correlated with the mean plumage spottiness of their mates ($r = .02$, $p = .84$, $n = 73$). Second, the mates of adult males were not more spotted than those of yearling males (Student's t test: $t_{100} = 0.08$, $p = .94$). In that analysis males captured at first-year of age appeared only in the category "yearling" ($n = 48$) and other males only in the category "adult" ($n = 54$). Third, when a male changed mates, it did not acquire a new female that was more spotted than the previous one (mean $\pm$ 1 SD female plumage spottiness = 1.93 $\pm$ 0.69 versus 1.77 $\pm$ 0.62; paired t test: $t_{41} = 1.4$, $p = .16$).
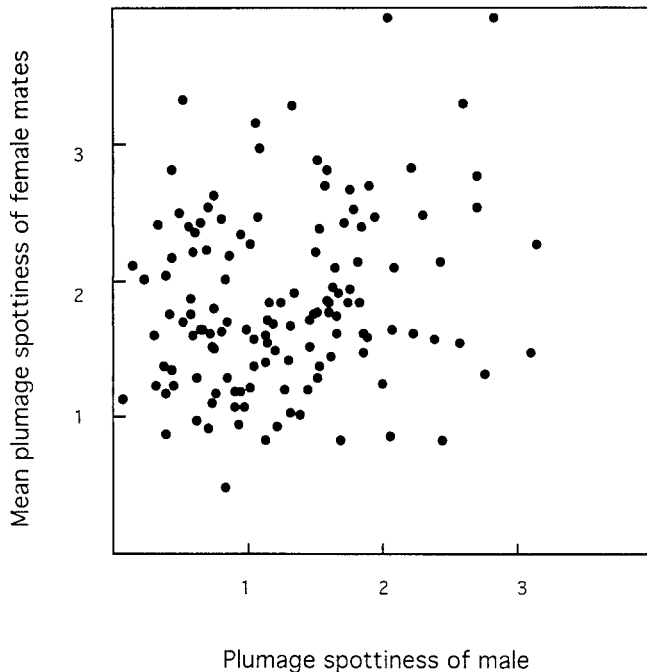
Figure 4
Assortative mating with respect to plumage spottiness.

Figure 5
Male and female feeding rates in relation to the manipulation of the female plumage spottiness in 1997. Bars represent means ±1 SE.

The same analysis repeated on a subsample of these males (i.e., those that bred at first and second year of age with different females) provided a similar result ($t_{12} = 0.07$, $p = .95$). Therefore, male body size, plumage coloration, and experience did not seem to have an influence on the kind of female a male acquired. In contrast to the present study, in the barn swallow repeatability of female pairing with respect to male tail length may have arisen because the phenotypic quality of the choosy sex influences mate sampling. Condition of female barn swallows was shown to be important in acquiring long-tailed males (Møller, 1991), and, thus, if condition is stable over years, individual females may be expected to get a new male displaying a tail of similar length as the previous mate.

Hypothesis 3: variation in male mate preference
The last hypothesis proposes that under the same pairing options different males chose differently spotted females. Variation in mate preference may be heritable (reviews in Bakker and Pomiankowski, 1995; Jennions and Petrie, 1997) or influenced by the parental phenotype when individuals prefer partners that resemble their opposite-sex parent without any genetic basis (sexual imprinting: Bateson, 1983; Ten Cate and Bateson, 1988). Two outcomes are expected when variation in male mate preference is maintained in a population.

First, the pairing decisions of sons and fathers should be similar because they share genes coding for a pairing preference or because a preference is transmitted between them via the mother's plumage characteristics. Thus, the mates of sons and fathers should resemble each other with respect to plumage spottiness. To evaluate this hypothesis, I averaged the plumage spottiness of all mates of a father, respectively of his sons. In the case when a father recruited more than one son, I averaged the values of brothers. The resemblance between father's and sons' mates was significant ($r = 41\% \pm 17\%$, $F_{24, 25} = 2.4$, $p = .018$; Figure 3). Similar findings for female preferences for ornamented males has been reported under laboratory conditions (Bakker and Pomiankowski, 1995), and
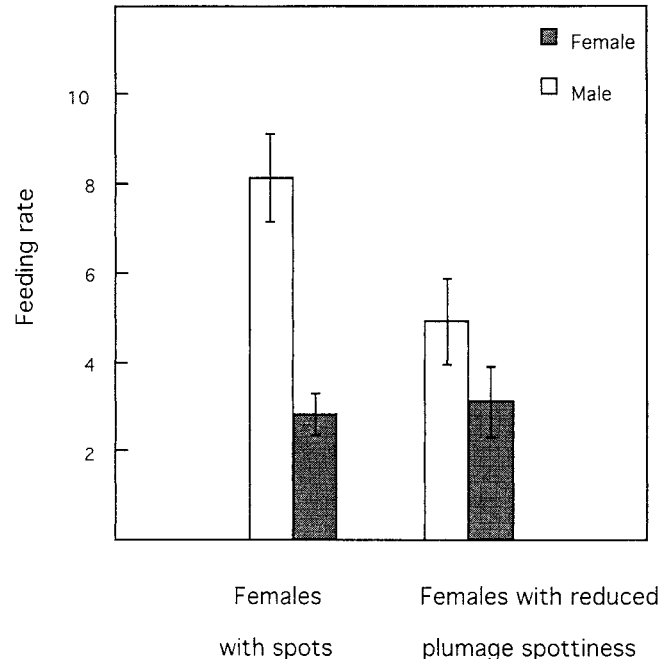
only one study previously tested in birds whether the pairing pattern of parents and same-sex offspring was the same, but the results were equivocal (Johnson et al., 1993).

Second, because mothers transmit genes coding for plumage spottiness to sons (unpublished data), the magnitude of male mate preference may be related to male plumage spottiness or, in other words, the preference and the preferred trait may be genetically or phenotypically correlated within males. Empirically such a phenotypic correlation could be suspected if pairing is assortative with respect to plumage spottiness (Johnson et al., 1993). I found a significant positive relationship between male plumage spottiness and the mean plumage spottiness of all a male's mates (Pearson correlation: $r = .21$, $p = .015$, $n = 132$; Figure 4). It may be noted that assortative mating was weak but comparable with the one found for tail length in the barn swallow (Møller, 1993; linear regression with $R^2 = .09$).

In my study, the mechanism leading to assortative pairing was probably not mutual mate choice with respect to the mate plumage spottiness because the pairing pattern of females with respect to male plumage spottiness was not repeatable: based on 45 females that bred with 2–5 different males, females that changed mates were not seen acquiring a new mate that was similarly spotted as the previous one (repeatability, $r = 13\%$, $F_{44, 64} = 1.1$, $p = .32$). Moreover, it was probably not due to a relationship between female plumage spottiness and male phenotypic characteristics, because body size, plumage coloration, and age of the males were not related to their own plumage spottiness (Table 1) or to that or their females (see above). Thus, assortative mating with respect to plumage spottiness was presumably not the indirect consequence of assortative mating by size, plumage coloration, or age. Finally, assortative mating was probably not the result of an active (i.e., mate choice) or passive (e.g., the two subspecies live in different environments) avoidance of individuals of the subspecies *T. a. guttata* to pair with individuals of the subspecies *T. a. alba,* and vice versa. *T. a. guttata* are spottier than *T. a. alba,*
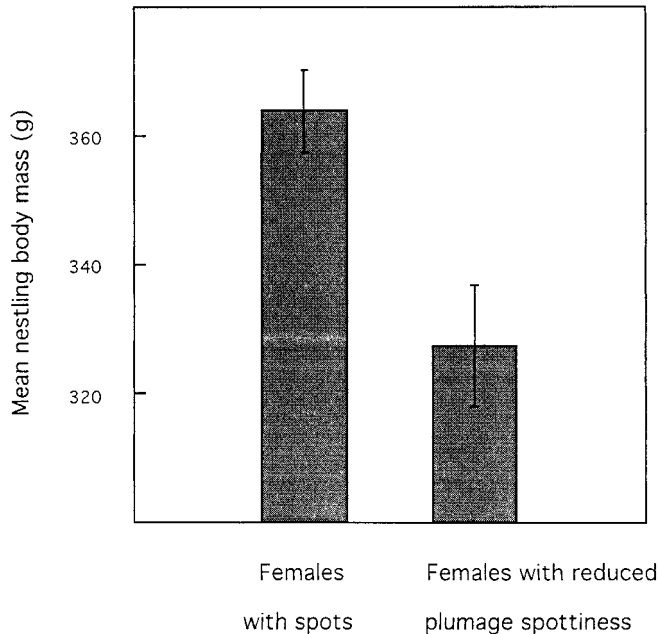
Figure 6
Mean nestling body mass (grams) in relation to the manipulation of the mothers' plumage spottiness. Nestlings were on average 34 days of age. Bars represent means ±1 SE.

a

Female plumage spottiness

b

but also more reddish-brown (Voous, 1950). Thus, if assortative mating with respect to plumage spottiness was due to assortative mating with respect to subspecies, I should have found assortative mating not only with respect to plumage spottiness but also with respect to plumage coloration. This was not the case (coloration: $r = .13$, $p = .14$, $n = 132$).

Experimental manipulation of female plumage spottiness

The experimental manipulation of female plumage spottiness significantly affected the feeding rate of males but not of females. Males mated to females with spots provisioned their broods on average more intensely than those mated to females with reduced plumage spottiness (Student's t test: $t_{26} = 2.33$, $p = .026$; Figure 5). Because females of both treatments fed their broods at a similar rate ($t_{26} = -0.31$, $p = .76$; Figure 5), the effect of the experiment on male feeding rate was probably due to the experimental manipulation of female plumage spottiness per se and not to a difference in female behavior.

Reproductive success differed between the two experimental treatments. Females with spots tended to produce more fledglings than females with reduced plumage spottiness (median brood size at fledging, 4 versus 3; Mann-Whitney U test, $U = 177$, $p = .13$, $n = 17$, 16), and fledging success was significantly higher in their nests (effect of the manipulation on the number of fledglings after controlling for the number of hatchlings, Kendall rank-order correlation, $\tau = -0.28$, $p = .02$, $n = 33$). The mean body mass of the surviving nestlings was larger in nests of females with spots than in nests of females with reduced plumage spottiness ($t_{29} = 3.31$, $p = .003$; Figure 6). This effect remained significant after controlling for brood size as a covariate (ANCOVA, $F_{1,28} = 13.5$, $p < .001$). In conclusion, females with reduced plumage spottiness achieved a lower fledging success and produced offspring with lower body masses than females with spots, probably because of a reduction in the male feeding cadency. This experiment
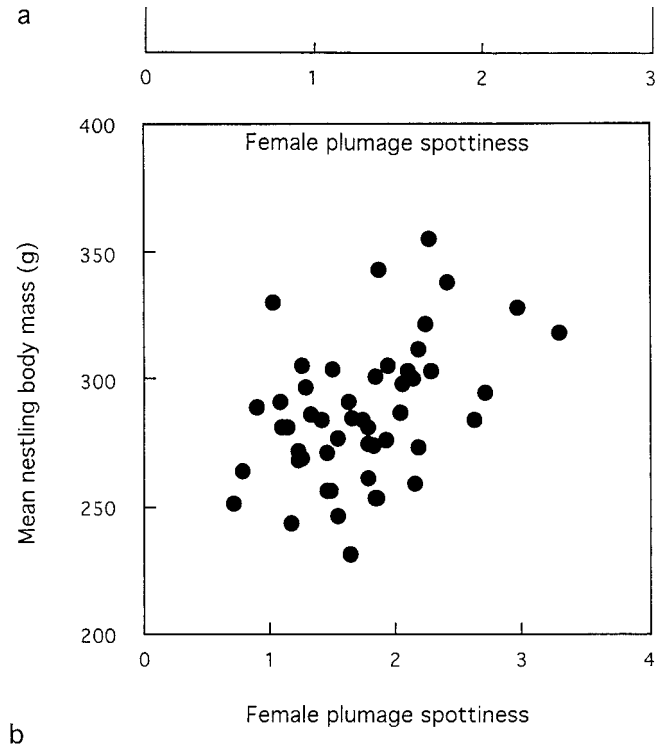

Figure 7
Relationship between the mean nestling body mass (grams) and the natural expression of female plumage spottiness in (a) 1996; nestlings were on average 25 days of age and (b) 1998; nestlings were on average 40 days of age.

further suggests that males assess the plumage spottiness of their mates even during the rearing of the young.

There may be at least two explanations for why paternal investment was negatively affected by the removal of black spots on females' plumage. First, males may have reduced

feeding rate because they did no more recognize their mates (Whitfield, 1986). No data are yet available to discuss this possibility. Second, males may invest less effort in reproduction when mated to a heavily spotted female than to a sparsely spotted one (de Lope and Møller, 1993; Møller, 1994b). This hypothesis predicts that in unmanipulated populations males mated to heavily spotted females bring more food to the nest than those mated to sparsely spotted females.

To examine this prediction, I correlated nestling body mass to plumage spottiness of the mother. Because males bring twice as many prey items to the nest than females (Figure 5), nestling body mass can be considered an index of paternal investment (see also Roulin et al., in press). In 1996, nestlings were heavier when raised by more heavily spotted females ($r = .43$, $p = .002$, $n = 50$; Figure 7a). This positive relationship was not due to a seasonal effect (correlation between hatching date of the first offspring and female plumage spottiness: $r = -.10$, $p = .50$, $n = 50$) or to the production of smaller broods by more heavily spotted females ($r_s = -.12$, $p > .20$, $n = 50$). In 1998, the same relationship was found between mean nestling body mass and female plumage spottiness ($r = .40$, $p = .012$, $n = 40$; Figure 7b), and again there was no relationship between female plumage spottiness and hatching date ($r = .0$, $p = 1.0$, $n = 40$) or brood size ($r = -.03$, $p = .86$, $n = 40$). Without excluding that female plumage spottiness is used as an individual recognition system, these correlations may suggest that in the above experiment, males reduced parental investment because they invest more effort in reproduction when mated to heavily spotted females.

Conclusion

Barn owls displayed repeatability of male pairing with respect to a plumage trait exhibited by females. The results suggest that nonrandom male pairing was neither due to a nonrandom distribution of the females among nest sites nor to age and morphological characteristics of the males. The correlational data presented here may suggest the existence of variance in male preference for female plumage spottiness. This variance might be genetic or might be caused by sexual imprinting. An experiment where female plumage spottiness was reduced after mating altered male feeding rate and reproductive success, suggesting that males assess the plumage spottiness of their mates. Experiments are now required to test whether males derive fitness benefits by pairing nonrandomly and whether female plumage spottiness is a signal of quality.

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