Male ornament size as a reliable cue to enhanced offspring viability in the barn swallow

(female choice/good genes models/sexual selection)

ANDERS PAPE MØLLER

Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden

ABSTRACT   Many extravagant secondary sexual characters are assumed to have evolved as a result of female choice, either because they attract females or because they reliably reflect the quality of males. Females mating with the most ornamented individuals with a superior genotype are expected to benefit by producing more viable offspring. A viability advantage associated with mate choice can be demonstrated only if (i) parent ornament size reliably reflects parent viability and (ii) offspring viability is directly related to the expression of the ornament of the parent. Barn swallows (Hirundo rustica) are monogamous passerine birds, which are sexually size dimorphic in tail length. Previous experiments and observations have shown that females prefer males with the largest tail ornaments and that male survivors have larger tail ornaments than nonsurvivors. Here I demonstrate that offspring longevity is positively related to ornament size of the male parent and that the longevity of sons is a trait with a statistically significant resemblance to that of their fathers. The viability effects could be entirely due to differences in quality of parental care. However, relative paternal provisioning of offspring was negatively related to the tail length of males, while total provisioning rate by both pair members, and thus offspring body size, body mass, and body condition, was unrelated to male tail length. Therefore, females may, through their mate choice, gain an indirect fitness advantage in terms of enhanced offspring viability.

Females may choose mates to produce male offspring with so-called arbitrary sexy traits (1–4), or they may choose mates of generally high viability as advertised through an extravagancy of secondary sexual characters (5–10). A clear distinction between these two groups of models is that the good genes models predict viability to be positively related to the expression of the sexual ornaments (5–11), while such a relationship is not predicted by the arbitrary trait models. Several field studies have demonstrated that male viability is directly related to degree of ornamentation (11–16). However, as far as free-living animals are concerned, no evidence exists to prove that offspring longevity is positively related to the degree of ornamentation of their fathers. Here I report such a relationship in the monogamous barn swallow (Hirundo rustica).

Barn swallows are small (≈20 g), monogamous, insectivorous passerines that feed on the wing and usually nest in small colonies. Sexual size dimorphism is large only for the outermost tail feathers, which on average are 16% longer in adult males than in adult females (17, 18). Tail length increases slightly among males from their first to their second year, but individual males are almost equally consistent in their tail length between years independent of whether age effects are controlled (18). Naturally and experimentally

long-tailed males are more likely to attract a mate than are short-tailed males; moreover, long-tailed males acquire mates more quickly than those short-tailed males that succeed in mating (17, 19). As a result, long-tailed males produce offspring that fledge sooner and these males also father second clutches more frequently than short-tailed males (17, 19).

METHODS

Barn swallows were studied at Kraghede (57°12' N, 10°00' E), Denmark, in an open farmland habitat with scattered plantations, ponds, and hedgerows, where they breed on farms either solitarily or in colonies of up to 50 pairs. The largest majority of birds breed in colonies of >10 pairs. I visited all previously used nest sites almost daily throughout the breeding seasons of 1984–1989 and in 6 weeks during 1990–1991. Barn swallows were captured in mist nets at the breeding sites or, less frequently, with sweep nets at night while roosting within their breeding territory. No birds deserted their breeding site after capture. All barn swallows were provided with a numbered aluminium ring, and >98% of all individuals were eventually captured as determined by the frequency of unringed birds at the breeding sites.

Barn swallows were sexed by means of the presence (female) or absence (males) of a brood patch and by the shape of their cloacal protuberance, which is considerably larger in males. I measured the length of the two outermost, elongated tail feathers (to the nearest mm) and a number of other standard morphological measurements (see ref. 18 for a full description of the methods). Tail length was defined as the average length of the two outermost tail feathers. All barn swallows involved in field experiments were excluded from all present analyses, but this does not bias the remaining sample in any particular way, because experimental individuals were picked at random.

The birds were classified as either yearlings, if they had not bred previously in the study area, or as 2 years old or older, if they had done so at least once. Since breeding dispersal of the barn swallows is very limited (only 3 of 401 birds have moved from one farm to another, the maximum distance dispersed being 300 m), birds being caught for the first time can safely be assumed to be yearlings. This conclusion is further supported by recaptures of 98 barn swallows ringed as nestlings and subsequently found breeding in the study area, as all of these were first recaptured as yearlings. I was able to recapture most returning individuals, since only 6 of 401 adult birds were not captured in 1 year but were so in the subsequent year. Longevity was estimated as the number of years spent in the study area. I therefore excluded all individuals still alive during the 1991 breeding season from my analyses. Since there is a strong sex bias in natal dispersal, females dispersing farther than males, I have

Abbreviation: ANCOVA, analysis of covariance.

restricted the analyses to the sample of male offspring. Natal dispersal distances in barn swallows are large and <1% of all ringed nestlings recruit in the study area. The number of recruits from the different years was as follows: 1984, 2; 1985, 3; 1986, 2; 1987, 2; 1988, 25; 1989, 2; and 1990, 0. The breeding season of 1988 was by far the best season during the study period; many nestlings were produced and their body condition was better than in any of the other years (unpublished data). Most barn swallows breed in colonies of >10 pairs (87% of the barn swallows) and most of the recruits (35 of 37 male recruits) also came from these colonies.

The major contribution of males to reproduction is their feeding of offspring, and they on average contribute slightly less than half of the total number of feedings. Feeding rates for males and females were recorded during 1-hr daily observation periods throughout the nestling period, a task facilitated by the fact that barn swallows were used to the presence of humans at the farm breeding sites. Most observations were therefore made at close range, usually at a distance of <5 m. The sex of parents providing food could easily be determined from the length of the tail feathers and the color rings. Each brood was observed a total of 16–27 hr, depending on the duration of the nestling period. Such daily 1-hr observations of feeding activity provide consistent estimates of parental care, since feeding rates of individuals in the morning also were representative for feeding rates at noon and in the evening (20). Kendall coefficients of concordance for male feeding rates and percentage of male feedings (percentage of all feedings provided by the male) were large and highly significant (20). Daily estimates of feeding rates were later reduced to a mean feeding rate for the male parent for the entire nestling period.

The calculated relative male feeding rate will only provide an accurate estimate of reproductive effort if there is no significant relationship between feeding rate and the amount of food provided per visit. I tested this assumption during the 1988 breeding season by sampling food boluses brought during calm weather from 0900 to 1200 hr to nestlings aged 8–12 days from 42 first broods and by recording feeding visits during a 1-hr observation period (21). There was in fact no relationship between feeding rate and the amount of food provided per visit for male feeding rate, female feeding rate, or percentage of male feedings (22).

Tarsus length of offspring, which is a skeletal measure of adult body size kept throughout life, was measured with a digital ruling caliper to the nearest 0.01 mm when nestlings were 15 days old. Body mass of offspring was measured on a Pesola spring balance with an accuracy of 0.1 g when nestlings were 15 days old. Body condition is the residual from a linear regression of body mass on (tarsus length)^3. All three measures were reduced to a mean value per brood.

RESULTS

There was a direct positive relationship between offspring longevity and the degree of ornamentation of their fathers measured in terms of tail length (Fig. 1A). Male offspring of long-tailed male barn swallows lived longer than did male offspring of short-tailed male barn swallows. This was the case irrespective of whether the age of the father was taken into account (multiple regression analysis: $F = 15.42$; df = 2, 32; $P < 0.0001$; tail length of father: β (standardized regression coefficient) = 0.53, $P = 0.0004$; age of father: $\beta = 0.20$, $P = 0.15$). An increase in male tail length by 1.94 SD (mean tail length of fathers in the present sample [($n = 37$) was 106.7 mm (7.2, SD)] was associated with an increase in offspring life expectancy by 1 year.

Long-tailed male barn swallows acquire mates that survive better than females mated to short-tailed males (23), and it is possible that the enhanced viability of sons derived from the
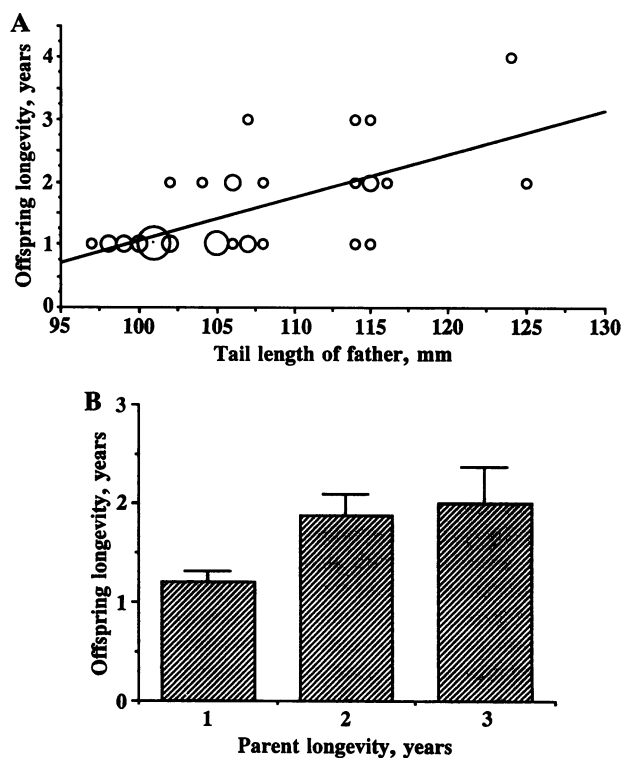

FIG. 1. (A) Longevity of male barn swallow offspring in relation to the tail length (mm) of their father. The relationship is statistically significant ($F = 24.59$; df = 1, 33; $P < 0.0001$), while the effect of the year when the offspring was reared is unimportant ($F = 0.25$; df = 1, 33; $P = 0.62$). The regression equation is offspring longevity = 0.070 (SE = 0.014) tail length of father −5.91 (SE = 1.49). Circles of increasing size represent one, two, three, and four observations, respectively. The tail length of the father originates from the year when the offspring in the data set was reared. All fathers were only represented once in the data set. (B) Longevity of male barn swallow offspring in relation to longevity of their father. Values are means + 1 SE. The relationship is positive and statistically significant ($F = 8.90$; df = 1, 33; $P = 0.0053$), while the effect of the year when the offspring was reared is unimportant ($F = 0.016$; df = 1, 33; $P = 0.90$).

father, the mother, or both. I tested these possibilities in an analysis of covariance (ANCOVA) with longevity of sons as the dependent variable, the year when the son was reared as a factor, and tail length of the father and the mother as covariates. This procedure was justified because female tail length is known to reflect female reproductive potential in terms of timing of breeding, number of broods per season, and quantity of offspring raised (24). The ANCOVA therefore tests whether male tail length, female tail length, or both are reliable predictors of the longevity of sons. There was a significant positive effect of the tail length of the father ($F = 9.95$; df = 1, 32; $P = 0.0035$), but a much weaker and nonsignificant effect of the tail length of the mother ($F = 2.34$; df = 1, 32; $P = 0.14$), while the year effect was nonsignificant ($F = 0.21$; df = 1, 32; $P = 0.65$). This result strongly suggests that the viability effect derives from the father rather than the mother.

Since male barn swallows with long ornaments generally are more long-lived than males with short tail ornaments (11), and since male offspring of long-tailed males also live longer than male offspring of short-tailed males, sons should resemble their fathers with respect to longevity. I estimated the resemblance of longevity in an ANCOVA with longevity of male offspring as the dependent variable, the year when offspring was reared as a factor, and longevity of the father as a covariate. The resemblance between sons and fathers was strong (Fig. 1B; $F = 8.90$; df = 1, 33; $P = 0.0053$). Thus

Evolution: Møller

Proc. Natl. Acad. Sci. USA 91 (1994) 6931

male offspring resemble their fathers with respect to longevity.

Similarity in life-span between sons and fathers may depend on genetic variation or on similarities in the environment. I investigated the effect of four obvious environmental factors—a common breeding environment, parental care, rearing conditions, and the distribution of males with different tail lengths or ages across colonies of different sizes—but none of these was able to account for the similarity in longevity. First, sons are likely to experience an environment more similar to that of their father if they only disperse a short distance before settling to breed. The sons included in the present study dispersed, on average, 1.69 km (SE = 0.13; range, 0.4–4.7 km; $n = 37$). I investigated the effect of natal dispersal distance on longevity in an ANCOVA with longevity of sons as the dependent variable, year of rearing of sons as a factor, and longevity of fathers and natal dispersal distance of sons as covariates. There was a positive effect of the longevity of fathers on that of sons ($F = 8.73$; df = 1, 32; $P = 0.0058$), while the effects of natal dispersal distance and year of rearing were unimportant (dispersal distance: $F = 0.15$; df = 1, 32; $P = 0.70$; year of rearing: $F = 0.04$; df = 1, 32; $P = 0.84$). Similarities in breeding environment between fathers and sons as measured from natal dispersal distance of sons thus did not account for the resemblance in longevity between fathers and sons.

The relationship between offspring longevity and paternal ornament size might stem from differences in the quality of parental care (review in ref. 4). I tested this second hypothesis by determining the relationship between tail length of male barn swallows and food provisioning of their offspring. I recorded provisioning of nestlings by male and female parents in 131 barn swallow pairs (22). The percentage of all feeding visits provided by the father was negatively related to his tail length in the first and the second clutch (Table 1). However, total provisioning rate by the parents was unrelated to the males' tail length (Table 1). Body size of offspring measured as tarsus length was therefore also unrelated to the tail length of their father (Table 1). Similarly, offspring body mass, which predicts survival prospects (25), and offspring body condition were unrelated to tail length of the father (Table 1).

Third, I tested whether ornament size in male barn swallows was related to measures of their rearing condition such as the rearing date, the number of siblings (brood size), or the male parents' age. Ornament size of males was not significantly related to any of these variables (rearing date: β (standardized regression coefficient) = 0.12, $n = 37$, $P = 0.21$; brood size: $\beta = 0.06$, $n = 37$, $P = 0.72$; male parents' age: $\beta = 0.10$, $n = 37$, $P = 0.32$). These results suggest that the offspring of long-tailed males did not on average experience superior rearing conditions than the offspring of short-tailed males.

Fourth, I tested whether males of different ages or tail lengths were distributed randomly across colony sizes, since this factor could be important if particular colony sizes were better rearing sites. The relationship between male features and colony size was investigated in ANCOVAs with year as a factor, because the relationships are likely to vary between years. However, there was no relationship between male tail length and colony size ($F = 1.01$; df = 1, 523; $P = 0.32$), while the year effect was statistically significant ($F = 3.38$; df = 7, 523; $P = 0.002$). Similarly, there was no statistically significant relationship between male age and colony size ($F = 0.71$; df = 1, 381; $P = 0.40$), while the year effect was statistically significant ($F = 2.25$; df = 1, 381; $P = 0.03$). These analyses suggest that heterogeneity in the distribution of males varying in tail length or age across colony sizes cannot account for the relationships between male tail length and longevity and offspring viability.

DISCUSSION

The main findings of this duty are that (*i*) male barn swallows with long tails recruit long-lived male offspring and (*ii*) there is a statistically significant resemblance in longevity between male parents and their sons. These results can be due to at least three different effects. First, female barn swallows may obtain a viability advantage for their offspring by choosing males with the most extravagant tail ornament, as suggested by the good genes models of sexual selection (5–9). Two laboratory studies of *Drosophila* have previously demonstrated viability effects of mate choice in offspring (26, 27), but causes of mortality that are important in the field may have been excluded in the laboratory setting. A recent field study of great tits (*Parus major*) suggests that male ornamentation directly affects offspring viability (16). One previous study has estimated the heritability of longevity in a free-living bird, the collared flycatcher (*Ficedula albicollis*), and it was very close to zero (28). Experimental studies of *Drosophila* have shown that the genetic variance in longevity is enhanced under stressful environmental conditions, while the genetic variance is relatively low under more benign conditions (29). The barn swallow and the collared flycatcher differ in one important respect; while sexual selection is strong and directional in the barn swallow, selection on plumage coloration in the collared flycatcher appears to be weak (L. Gustafsson, personal communication). Strong sexual selection may lead to a coupling between genes for viability and genes affecting the expression of a secondary sexual character (5, 6, 8, 9). Directional selection may increase the genetic variance because of linkage between viability genes and genes affecting the expression of the sex trait and because of selection against modifier genes that control the development of the secondary sex trait. It is possible that the large resemblance in longevity between fathers and sons in the barn swallow could be due to the linkage between the degree of male ornamentation and male viability and to assortative mating with respect to viability. Alternatively, collared flycatchers and barn swallows may differ in the extent to which they are subject to selection from parasites or other kinds of antagonists. The secondary sex

Table 1. Relationships between tail length, age, and brood size of male barn swallows and the relative and absolute feeding rates and body size, mass, and condition of their offspring, respectively.

Dependent variable	Tail length		Age	Brood size
First clutch ($n = 131$)				
% male feedings	−0.28*	(−0.19)*	−0.003	0.003
Total feeding rate	0.05	(0.03)	0.32	0.96
Tarsus length	0.003	(0.04)	0.14	−0.006
Body mass	0.01	(0.12)	0.24	−0.24
Body condition	−0.02	(0.005)	−0.40	−0.18
Second clutch ($n = 90$)				
% male feedings	−0.21*	(−0.18)*	−0.001	0.02
Total feeding rate	0.09	(0.04)	−0.11	0.42
Tarsus length	−0.004	(−0.22)	0.21	−0.06
Body mass	0.0002	(0.04)	−0.04	0.12
Body condition	−0.002	(0.08)	0.32	0.15

Values are standardized regression coefficients from an ANCOVA with year as the factor and tail length, age, and brood size of male barn swallows as covariates (with values from the simple univariate linear regression between the dependent variables and male tail length in parentheses). Each male barn swallow was only represented once in the data set.

*$P < 0.05$.

traits of barn swallows may therefore have evolved as a consequence of high levels of parasite infestations, and only the most resistant males, which for that reason would also be the most long-lived individuals, would be able to develop large secondary sexual characters (7). Long tails in barn swallows would therefore be revealing handicaps causing positive correlations in viability across generations, while the absence of revealing handicaps in collared flycatchers would cause a lack of correlation in viability across generations.

Second, the resemblance in longevity between fathers and sons could be entirely environmental. I have previously demonstrated that perferred males acquire mates of phenotypically high quality, and these females invest differentially in reproduction without reducing their survival prospects (24). I attempted to control statistically for this effect in a number of different ways in the present study. (*i*) Total provisioning rates of offspring during the nestling period and subsequently offspring quality in terms of body size and body condition were unrelated to tail length of the father. (*ii*) Ornament size of male barn swallows was unrelated to rearing conditions as determined by rearing date, number of siblings, and parent age. (*iii*) Because natal dispersal distance could be determined by nestling quality, I determined the effect of dispersal distance on longevity. However, there was no such effect of dispersal. These analyses rule out a number of obvious explanations although, of course, they cannot rule out all effects of rearing conditions.

Third, the resemblance in longevity of fathers and sons could be accounted for if there was a considerable bias in the barn swallow data set. For example, it is known that elimination of a fraction of offspring through mortality may affect parent–offspring resemblance in the rest of the population (30). This could easily be the case in the barn swallow because <1% of the nestlings later recruit into the study area. Inclusion of individuals recruiting outside the study area may result in a different parent–offspring resemblance if the locality of recruitment was dependent on offspring phenotype. Analysis of natal dispersal suggests that this explanation is unlikely. Three other effects of bias can also be excluded. (*i*) Heterogeneity among years does not affect the resemblance since there was no effect of year on the relationship. (*ii*) Colony size apparently does not affect the resemblance since male barn swallows differing in age and tail length were randomly distributed across colony sizes. (*iii*) Dispersal distance does not cause any bias in the resemblance. In conclusion, there was no bias due to the most obvious possibilities, although it cannot be ruled out that other factors may have influenced the resemblance between fathers and sons.

In conclusion, the exact nature of the viability advantage in the barn swallows could be entirely environmental, genetic, or a combination. Searches for an effect of the most obvious environmental explanations were unsuccessful. The alternative explanation is that the enhanced viability of male offspring of long-tailed male barn swallows has a genetic basis. Small genetic differences among barn swallow nestlings—for example, in resistance to parasites (31)—may become amplified into large viability differences among adults, and this could account for the resemblance in longevity between fathers and sons.

1. Darwin, C. (1871) *The Descent of Man, and Selection in Relation to Sex* (John Murray, London).
2. Fisher, R. A. (1930) *The Genetical Theory of Natural Selection* (Clarendon, Oxford).
3. Kirkpatrick, M. (1982) *Evolution* 36, 1–12.
4. Kirkpatrick, M. & Ryan, M. J. (1991) *Nature (London)* 350, 33–38.
5. Zahavi, A. (1975) *J. Theor. Biol.* 53, 205–214.
6. Andersson, M. (1982) *Biol. J. Linn. Soc.* 17, 375–393.
7. Hamilton, W. D. & Zuk, M. (1982) *Science* 218, 384–387.
8. Kodric-Brown, A. & Brown, J. H. (1984) *Am. Nat.* 124, 303–323.
9. Pomiankowski, A. N. (1988) *Oxford Surv. Evol. Biol.* 5, 136–184.
10. Grafen, A. (1990) *J. Theor. Biol.* 144, 473–546.
11. Møller, A. P. (1991) *Proc. R. Soc. London B* 243, 145–148.
12. Alatalo, R. V., Höglund, J. & Lundberg, A. (1991) *Nature (London)* 352, 155–156.
13. Hill, G. E. (1991) *Nature (London)* 350, 337–339.
14. von Schantz, T., Göransson, G., Andersson, G., Grahn, M., Helgée, A. & Witzell, H. (1989) *Nature (London)* 337, 166–169.
15. Watt, W. B., Carter, P. A. & Donohue, K. (1986) *Science* 233, 1187–1190.
16. Norris, K. (1993) *Nature (London)* 362, 537–539.
17. Møller, A. P. (1990) *Anim. Behav.* 39, 458–465.
18. Møller, A. P. (1991) *Evolution* 45, 1823–1836.
19. Møller, A. P. (1988) *Nature (London)* 332, 640–642.
20. Møller, A. P. (1988) *Anim. Behav.* 36, 996–1005.
21. Møller, A. P. (1989) *Nature (London)* 339, 132–135.
22. Møller, A. P. (1992) *J. Evol. Biol.* 5, 603–624.
23. Møller, A. P. (1991) *Proc. R. Soc. London B* 245, 179–182.
24. Møller, A. P. (1993) *Evolution* 47, 417–431.
25. Magrath, R. D. (1991) *J. Anim. Ecol.* 60, 335–351.
26. Partridge, L. (1980) *Nature (London)* 283, 290–291.
27. Taylor, C. E., Pereda, A. D. & Ferrari, J. A. (1987) *Am. Nat.* 129, 721–729.
28. Gustafsson, L. (1986) *Am. Nat.* 128, 761–764.
29. Hoffmann, A. A. & Parsons, P. A. (1991) *Evolutionary Genetics and Environmental Stress* (Oxford Univ. Press, Oxford).
30. van Noordwijk, A. J., van Balen, J. H. & Scharloo, W. (1988) *Genet. Res.* 51, 149–162.
31. Møller, A. P. (1990) *Evolution* 44, 771–784.