The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study

José J. Cuervo,ᵃ Florentino de Lope,ᵇ and Anders Pape Møllerᵃ
ᵃDepartment of Population Biology, Zoological Institute, Copenhagen University, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark, and ᵇDepartamento de Biología Animal, Facultad de Biología, Universidad de Extremadura, Avenida de Elvas s/n, E-06071 Badajoz, Spain

The outermost tail feathers in male barn swallows (*Hirundo rustica*) are the target of a strong directional female mate preference. The tail ornament is also expressed in females, since females have considerably longer tails than juveniles, either due to (1) a strong genetic correlation between the characters in the two sexes, or (2) direct sexual selection on females. To discriminate between these two hypotheses, we manipulated the length of the outermost tail feathers in female barn swallows shortly after arrival by either shortening or elongating the outermost tail feathers, or maintaining their length among control individuals. Start of laying of the first clutch, reproductive performance, or provisioning of offspring did not show any significant differences among treatments. Original female tail length before manipulation was unrelated to reproductive performance, while male tail length explained some variation in the number of clutches and, to some extent, the total number of eggs laid per year. Females with longer tails arrived earlier at the breeding grounds. Manipulated female tail length was positively correlated to the tail length of their mates. Our results support the correlated response hypothesis but do not support the sexual selection explanation for the existence of exaggerated tail feathers in female barn swallows. *Key words:* barn swallow, female ornament, *Hirundo rustica*, reproduction, sexual selection, sexual size dimorphism. [Behav Ecol 7:132–136 (1996)]

Sexual size dimorphism may arise because of natural or sexual selection. The niche segregation hypothesis suggests that size dimorphism arises as a result of intersexual competition for food (Darwin, 1871). For example, the sexes of some species of woodpeckers with permanent territories have clearly different foraging niches (Ligon, 1968; Selander, 1966), and different natural selection pressures in these niches may give rise to sexual size dimorphism. Sexual size dimorphism then mainly arises in characters involved in foraging, such as beak dimensions. However, if sexual dimorphism does not develop until sexual maturity it is likely that sex differences can be attributed to sexual selection (Darwin, 1871).

Sexual selection may account for sexual size dimorphism in at least two different ways. First, the correlated response hypothesis posits that dimorphism is the result of a female morphological character developing as a correlated response to selection on males because of a strong genetic correlation between the sexes for the trait (Lande, 1980; Lande and Arnold, 1985). The female morphological trait is dragged along by sexual selection on the male trait, and the subsequent decrease in the size of the character in females is a very slow process governed by natural selection (Lande, 1980). The female trait is therefore supposed to be selectively neutral or even slightly detrimental.

The second sexual selection explanation for sexual size dimorphism (the ornament hypothesis) suggests that the female trait is an ornament currently under sexual selection because of female-female competition and/or male choice. The trait can then be considered to be adaptive in females as well as in males, and the most extreme expression of the trait will confer a selective advantage to members of both sexes (Muma and Weatherhead, 1989; Trivers, 1972). However, different in-

tensities of sexual selection will produce differential development of the trait in males and females. If the female trait currently is under sexual selection, it may either reflect reproductive or parenting ability as suggested by the good parent process (Grafen, 1990; Heywood, 1989; Hoelzer, 1989), attractiveness to individuals of the opposite sex as suggested by the Fisher process (Fisher, 1930; Kirkpatrick, 1982; Lande, 1981; Pomiankowski et al., 1991), or genetic quality as suggested by the good genes process (Andersson, 1982, 1986; Hamilton and Zuk, 1982; Iwasa et al., 1991; Kodric-Brown and Brown, 1984; Trivers, 1972; Zahavi, 1975).

The possession of long tail streamers in certain birds such as members of the families Meropidae, Coraciidae, and Hirundinidae has been attributed to a natural selection advantage due to the effects of long, outermost tail feathers on maneuverability or general flight performance (Balmford et al., 1993; Norberg, 1994; Thomas, 1993). Detailed aerodynamic analyses indicate that an elongated, forked tail provides individuals with an advantage in terms of natural selection. However, this hypothesis does not explain the evolution of sexual size dimorphism unless elongation of tail feathers leads to differences in the benefits achieved by individuals of the two sexes. Hence, both natural and sexual selection have to be invoked to explain the evolution of sexual size dimorphism.

Barn swallows (*Hirundo rustica*) only demonstrate slight sexual size dimorphism in morphology with the exception of the longest, outermost tail feathers which are considerably longer in males than in females (Cramp, 1985; de Lope, 1985; Møller, 1991b). Sexual size dimorphism varies in Europe from less than 5% in southern Europe to more than 20% in Scandinavia (Møller, 1995). Male tail ornaments are the target of a strong directional female mate preference (Møller, 1988, 1992b, 1994a). There is little evidence for the hypothesis that natural selection accounts for the maintenance of sexual size dimorphism in barn swallow morphology since the degree of dimorphism is smallest for morphological characters used

during foraging, such as the dimensions of the beak (Møller, 1994a). Juvenile barn swallows also have tail streamers, but there is no sexual size dimorphism, and their length is considerably shorter than that of adult males and females (Møller, 1994a). Hence, sexual size dimorphism in the outermost tail feathers does not develop until after completion of the first prenuptial molt in spring (Møller, 1994a). Juvenile morphology must be close to the optimum under natural selection, while the morphology of adults is affected by both natural and sexual selection. Therefore, sexual rather than natural selection has to be invoked as an explanation for the evolution and maintenance of sexual dimorphism in the length of the outermost tail streamers among adult barn swallows.

There are few studies of the expression of secondary sexual characters in females (Hill, 1993; Muma and Weatherhead, 1989; Møller, 1993) and even fewer experiments (Jones and Hunter, 1993). A number of predictions regarding the causes and consequences of tail length variation among female barn swallows allows discrimination among the different hypotheses. The correlated response hypothesis predicts a genetic correlation between tail length of males and females, and that long tail feathers do not imply any advantage for females in terms of sexual selection. A genetic correlation between tail length of males and females is also consistent with the ornament hypothesis, but it also predicts that long-tailed females should be at a selective advantage in terms of sexual selection. Hence, males should prefer to mate with long-tailed females, and these females should acquire a mate earlier than other females, resulting in assortative mating with respect to tail length. The selective advantage to choosy males could be in terms of high reproductive or parenting ability of chosen females (good parent process), and we should thus expect long-tailed females to lay larger or more clutches, have higher annual reproductive success, or provision their offspring better than short-tailed females. Therefore, experimental manipulation of the length of female tails should result in a reduction in reproductive or parenting performance, if tail length before manipulation was at a selective optimum. Alternatively, long tail streamers might reflect female genetic quality. If this was the case, female tail length should reflect female viability, for example, in terms of migratory ability and hence arrival at the breeding grounds and general survival ability. If female tail length was unrelated to their parenting ability or general viability, but there still was a male preference for long-tailed females, then the Fisher process could be invoked. The aim of this study was to test these predictions by experimental manipulation of tail length in female barn swallows.

METHODS

The barn swallow is a small (about 20 g), insectivorous passerine that feeds on the wing and usually nests in small colonies. Sexual size dimorphism is slight with the exception of the outermost tail feathers, which are longer in males than in females, and longer in females than in juveniles of either sex (Cramp, 1985; Møller, 1994a). The experiment was carried out at Badajoz, Spain, during the breeding season of 1994. The study areas are agricultural land with scattered groups of trees (de Lope, 1983), and birds use rooms in farm houses and other buildings for breeding. Colony size ranged from 3 to 28 pairs.

In this area swallows arrive from their West African winter quarters from the beginning of February. We caught birds and manipulated the outermost tail feathers in females from mid-February until mid-March 1994, when the first clutches were laid. Barn swallows were caught in mist nets placed across all windows and doors before dawn, and all individuals at these breeding sites were thus captured. Several morphological

measurements were taken and each bird was provided with a metal ring and a combination of colored plastic rings. After capture, we identified the nest and the mate of each bird using binoculars, and nest contents were checked every second day to assess in all clutches (up to three for each pair) the start of egg laying, clutch size, date of hatching, and brood size at fledging. For some pairs we also recorded feeding rates during 1 h observation periods between 1400 and 1900 h when chicks (first brood) were 9 to 15 days old (i.e., when nestling growth peaks and feeding rates reach a maximum).

Females were randomly assigned to three experimental groups: (1) shortened tail in which the two outermost tail feathers were reduced in length by 20 mm, (2) elongated tail in which the two outermost tail feathers were cut and a 20 mm piece was added, and (3) a control group in which tail length was not manipulated. The first group (shortened) had a 20 mm long piece of feather cut 10 mm from the base of each of the two outermost tail feathers. The apical part of the feathers was glued back on the original feather using cyanoacrylate super glue. The second group (elongated) had also the outermost tail feathers cut 10 mm from the base and then the 20 mm long piece of feather from the shortened group was glued between the basal and the apical pieces. Tail feathers were cut and glued near the base where feathers have their maximum width (Møller et al., 1995). The third group of females (control) was captured, measured, and ringed, as in the other two groups, but their tail feathers were not manipulated. We did not include a second control group, with feathers cut and glued again to control for treatment effects, because previous experiments have shown that treatment itself had no effect (Møller, 1988, 1992a). Most birds were captured before mating, but in case of doubt, tail length was not manipulated.

Statistical analyses were performed according to Sokal and Rohlf (1981) and Siegel and Castellan (1988). We tested whether response variables were normally distributed before making analyses of variance (ANOVA) and covariance (ANCOVA). The statistical tests used are two-tailed. Values are means (SE).

RESULTS

We captured a total of 95 male and 80 female barn swallows in three farms less than 5 km apart. Male outermost tail feathers (mean = 98.0 (.7) mm, $n = 89$) were 15.9% longer than those of females (mean = 84.5 (.6) mm, $n = 74$). A total of 48 females were randomly assigned to the three experimental groups. Mean tail length in the shortened group was diminished by 23.4% to 65.4 mm ($n = 16$), and in the elongated group was increased by 23.5% to 105.0 mm ($n = 15$). The mean tail length in the control group was 86.3 mm ($n = 17$). The three experimental groups had very different mean tail lengths after manipulation (Kruskal-Wallis test, $KW = 40.74$, df $= 2.44$, $p < .001$). Female tail length before and after manipulation was weakly positively correlated (Kendall rank order correlation coefficient, $tau = .29$, $n = 47$, $p < .01$).

We did not find any difference among farms for several morphological characters [tail length before manipulation, wing length, tarsus length, wingspan, body mass, tail fluctuating asymmetry (FA; unsigned left − right character size), wing FA, and tarsus FA] and reproductive parameters (start of laying of the first clutch, number of clutches, number of successful clutches, total number of eggs, and total number of fledgings) for the female swallows involved in the experiment (one-way parametric or Kruskal-Wallis ANOVAs, $.32 \leq F \leq 2.54$, $1.43 \leq KW \leq 3.99$, df $= 2.44$ for tail length, tarsus length, tail FA, and tarsus FA, df $= 2.45$ in all other cases, $.09 \leq p \leq .73$). In view of these results, we pooled the data from the three localities for subsequent analyses. To ensure that we
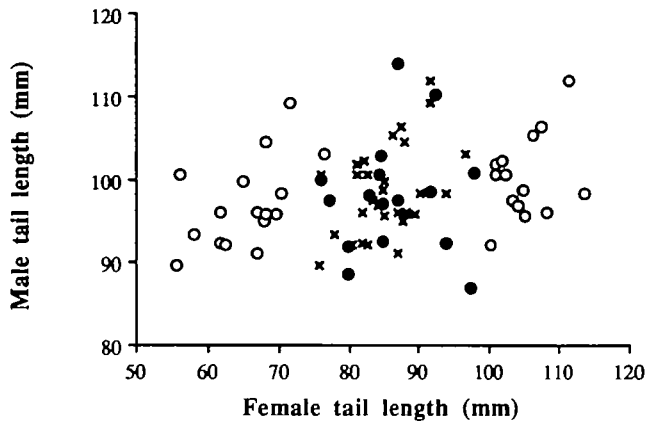
Figure 1
Tail length of male barn swallows in relation to the tail length of their mates before (crosses) and after (open circles) manipulation. Control birds are represented by a cross and a circle; their tail length remained constant.

Table 1
Effects of treatment, unmanipulated female tail length, and unmanipulated male tail length on reproductive performance (n = 46) and offspring provisioning (n = 36) of female barn swallows

Reproductive parameter	Treat-ment	Female tail length	Male tail length	Error
Start of laying	78.47	71.60	150.80[a]	46.61
Total number of eggs	1.27	.93	44.80[a]	11.28
Total number of fledglings	10.12	.48	3.83	12.11
Relative feeding rate	9.93	431.61	55.44	154.28
Feedings per chick	.41	1.46	.08	4.50

Values are mean squares from an ANCOVA.
[a] $p < .10$ for F ratios.

did not introduce any bias, when randomly assigning birds to the treatments, we compared morphological characters and date of manipulation among groups. No statistically significant differences were found (one-way parametric or Kruskal-Wallis ANOVAs, $.0005 \leq F \leq 1.01$, $.007 \leq KW \leq 2.47$, df = 2.44 for tail length, tarsus length, tail FA, and tarsus FA, df = 2.45 in all other cases, $.29 \leq p \leq 1.00$).

If tail-elongated females were preferred as mates by males, then their premating period (from arrival until mating) should be shorter than that of tail-shortened females. Since we could not accurately assess the duration of the premating period, the only parameter that allowed us to indirectly infer the length of this period was the start of laying of the first clutch (which is strongly positively correlated with arrival date; Møller, 1993). The differences in start of laying among the three groups of females were small and far from statistically significant (one-way ANOVA, $F = 0.36$, df = 2.45, $p = .70$). This result does not suggest that males preferred females with experimentally elongated tails.

If female tail length reflected their reproductive ability, we would expect reproductive performance to be inversely related to tail length after manipulation. However, reproductive performance did not differ among the groups of females: the number of clutches, the number of clutches with fledglings, the total number of eggs per season, and the total number of fledgings per season did not vary among the three groups (one-way parametric or Kruskal-Wallis ANOVAs, $.11 \leq F \leq 1.62$, $.28 \leq KW \leq 3.34$, df = 2.45, $.19 \leq p \leq .89$). Therefore, there was no evidence that female tail length reflected reproductive ability.

If female tail length reflected their ability to provision offspring, we predicted that female provisioning rate should be inversely related to experimental tail length. However, provisioning of offspring, measured as feeding rate by the female and number of feedings by the female per chick, was similar among treatments (one-way ANOVAs, $.05 \leq F \leq .07$, df = 2.34, $.93 \leq p \leq .95$). This suggests that female tail length was an unreliable predictor of female provisioning rate.

In previous studies tail length of male barn swallows have been shown to be positively correlated with that of their mates, even when the effect of age was controlled statistically (Møller, 1993). The correlation between unmanipulated tail length of females and that of their mates was positive, but nonsignificant for the sample of birds involved in the present experiment (Pearson product moment correlation coeffi-

cient, $r = .25$, $n = 46$, $p = .10$). Using tail length after manipulation instead, a significant positive correlation appeared (Kendall rank order correlation coefficient, $tau = .23$, $n = 46$, $p = .026$) (Figure 1). Unmanipulated tail length of female barn swallows was negatively correlated with date of first capture, which can be considered an estimator of arrival date (Kendall rank order correlation coefficient, $tau = -.27$, $n = 67$, $p < .01$). Therefore, females with long tails arrived at the breeding grounds earlier than those with short tails.

Female tail length before manipulation and male tail length could reflect subsequent reproductive performance of females, if tail length was a reliable indicator of female and male phenotypic quality. We tested this prediction by comparing experimental groups using ANCOVAs, with treatment as a factor and unmanipulated female tail length and male tail length as covariates. No significant differences among experimental treatments was found for reproductive parameters or provisioning of offspring (Table 1). To test for the possible relationships between tail length and the number of clutches, after controlling for the potentially confounding effect of the tail length of the mate, we performed Kendall partial rank order correlation analyses within each treatment group. The unmanipulated tail length of females was unrelated to reproductive performance or provisioning (Table 1) (for number of clutches and number of successful clutches: Kendall partial rank order correlation coeficient, $-.16 \leq partial tau \leq .27$, $n = 14$ for elongated group, $n = 16$ for shortened and control groups, $.15 \leq p \leq .85$). However, the tail length of males was positively correlated with the total number of clutches in the elongated (Kendall partial rank order correlation coefficient, $partial tau = .45$, $n = 14$, $p = .013$) and the shortened group ($partial tau = .43$, $n = 16$, $p = .019$), although not in the control group ($partial tau = .003$, $n = 16$, $p = .99$). Considering number of successful clutches the correlations were not significant ($.07 \leq partial tau \leq .36$, $n = 14$ for elongated group, $n = 16$ for shortened and control groups, $.07 \leq p \leq .73$). With regard to the other variables in the ANCOVA, tail length of males was not significantly related to reproductive performance or provisioning (Table 1). If considering manipulated tail length of females rather than their original tail length and tail length of males in the previous analyses, the results are almost identical.

DISCUSSION

Our experiment revealed no evidence for tail length in female barn swallows being maintained by a male preference for long-tailed females, since manipulation of female tail length did not affect their breeding date. Previous studies on female secondary sexual characters in some birds have reached

mixed conclusions. Muma and Weatherhead (1989) showed that the size of epaulets of female red-winged blackbirds (*Agelaius phoeniceus*) apparently was not currently associated with female quality, reproductive performance, or mating characteristics. Hence, they concluded that the presence of epaulets in females was a result of a correlated response to selection on males, which use this trait in intrasexual competition. Hill (1993), studying house finches (*Carpodacus mexicanus*), found no relationship between female plumage coloration and overwinter survival, reproductive success, or condition, although males showed a significant preference for the oldest and the most brightly plumaged females. He extended the nonfunctional explanation for female ornaments to include male mate choice as a nonadaptive trait resulting from a correlated response to selection on females. Male crested auklets (*Aethia cristatella*) displayed more to female models with experimentally exaggerated crest feathers than to less exaggerated models, as did females to manipulated male models, confirming the idea that ornaments expressed similarly in the two sexes could be favored by mutual mating preferences (Jones and Hunter, 1993). Three out of four studies thus appear to be inconsistent with male mate choice explanations for the maintenance of exaggerated female secondary sexual characters.

A positive genetic correlation between the secondary sexual characters in males and homologous traits in females is consistent with sexual selection models of indirect fitness benefits in terms of sexual attractiveness and viability and with models based on direct fitness benefits. Positive genetic correlations between the sexes are common for morphological characters (Falconer, 1981), and such a positive genetic correlation has been shown for tail length in the barn swallow (Møller, 1993) by correlating the tail length of sons to that of their mothers and the tail length of daughters to that of their fathers (Falconer, 1981). The correlated response hypothesis posits that the variation in tail length among females is selectively neutral or detrimental, while the ornament hypothesis suggests that females with a long tail have a mating advantage because female trait size reflects parenting ability, female sexual attractiveness, or general viability. We will now discuss the evidence for the latter hypothesis.

If the good parent process is working in the barn swallow, long-tailed females would be at a selective advantage due to an increased ability to lay multiple clutches, achieve higher seasonal reproductive success, or better provision their offspring. Our results do not confirm any of these predictions. We found no significant differences among experimental groups of females for any of the reproductive parameters (Table 1), and original female tail length did not account for a significant proportion of the variance. Møller (1993) showed that seasonal reproductive success was positively correlated with tail length in a Danish population of female barn swallows, even after controlling for age and year effects, mainly because long-tailed females mated earlier, enabling them more often to lay second clutches. We did not find a reduced reproductive performance of females with experimentally elongated tail feathers, as predicted if unmanipulated female tail length reliably reflected their reproductive ability. Male tail length explained some of the variation in the number of clutches laid by the female in the present study. This result could be explained in at least three different ways. First, long-tailed males might be better providers of food for their offspring, releasing females from this task and allowing them to invest more in egg laying. There is no evidence that long-tailed male barn swallows are better food providers than short-tailed males in the present or any previous study (Table 1; Møller, 1994a). Second, long-tailed males might be able to attract mates in better condition which therefore would be

able to lay larger and more clutches. There is experimental and correlational evidence for this hypothesis from previous studies of the barn swallow (Møller, 1991a, 1994a). Third, females might invest more in reproduction when their mates are of higher quality; that is to say, females mated to long-tailed males would provide a relatively larger share of the total amount of food for the nestlings. Previous studies on barn swallows support this explanation (de Lope and Møller, 1993; Møller, 1992b, 1994b).

If the good genes process is working, long-tailed females would be chosen preferentially as mates because of their quality in terms of better survival prospects, superior migratory performance, or faster molt. We found that females with longer unmanipulated tails arrived earlier at the breeding grounds than short-tailed females, indicating that female tail length was a reliable predictor of migratory ability, corroborating the results of previous studies on barn swallows (Møller, 1994a). Survival prospects of female barn swallows was unrelated to tail length in previous studies of a Danish population (Møller, 1991c).

Even if female tail length did not reliably reflect reproductive or parenting abilities or genetic quality, it could still be the target of a male mate preference, as envisaged by the Fisher process. The lack of evidence of a mating advantage for females with elongated tails suggests that long tails in female barn swallows are not maintained by a male mate preference for attractive female secondary sexual characters.

If both male and female tail length reflects phenotypic or genotypic quality, and if there is mutual mate preferences for a secondary sexual character in both sexes, assortative mating with respect to the size of the secondary sexual character may be predicted (Møller, 1993, 1994a). Tail length of female barn swallows after manipulation was positively and significantly correlated with the tail length of their mates (Figure 1), although the relationship was weaker and statistically nonsignificant for unmanipulated female tail length. A positive correlation between tail length of male barn swallows and that of their mates, even after removal of possible effects of age, has been shown in a previous study of a Danish population (Møller, 1993). These results are consistent with assortative mating with respect to tail length. Alternatively, the positive correlation between tail length of males and that of their mates could be explained by long-tailed females arriving early and therefore being able to mate with long-tailed males. A male mate preference for long-tailed females thus is not a prerequisite for a positive correlation between the phenotype of males and that of their mates.

The long tail streamers of female barn swallows may give rise to natural selection advantages due to effects on maneuverability or general flight performance (Balmford et al., 1993; Norberg, 1994; Thomas, 1993). This hypothesis obviously has its limitations because it cannot explain sexual size dimorphism in tail length in the barn swallow. However, let us disregard this problem for the moment. If a long tail provides females with advantages in terms of maneuverability, manipulation of tail length should displace individuals from their chosen optimum and performance should therefore decrease after tail elongation or shortening. We found no evidence of female reproductive performance or provisioning being related to experimental manipulation. This result does not support the idea that female barn swallows gain advantages in terms of natural selection from their long outermost tail streamers.

None of our analyses shows a clear male preference for females with elongated tails, and female tail length did not appear to reflect reproductive or parenting abilities. Long-tailed females arrived earlier at the breeding grounds, but this did not give rise to earlier mating or laying. Since the outer-

most tail feathers of female barn swallows do not appear to be the target of a male mate preference, their presence seems to be a mere consequence of a genetic correlation between the tail length of males and females. Therefore, our experimental study supports the correlated response hypothesis for the maintenance of exaggerated tail feathers in female barn swallows more than any of the sexual selection hypotheses based on direct or indirect fitness benefits to choosy males.

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