

Experimental manipulation of tail length in female barn swallows (*Hirundo rustica*) affects their future reproductive success

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Previous studies have shown no significant effect of experimental tail length manipulation in female barn swallows (*Hirundo rustica*) at the beginning of a breeding season on reproductive success or behavior during that breeding season. In the present study, we investigate if tail length manipulation had any effect on reproductive performance the following year, the so-called long-term effect, in contrast to the short-term effects already studied. We found that females with experimentally elongated external tail feathers at the beginning of a breeding season produced less offspring during the breeding season the following year than did females with shortened or unmanipulated tails. These results suggest that tail elongation caused flight deficiencies that deteriorated the condition of females and eventually reduced reproductive success. The finding of long-term effects but no significant short-term effects for female tail elongation suggests that female barn swallows have the ability to adjust immediate parental investment. Detrimental effects of long tails in females in terms of decreased reproductive success might explain why female tails are not as long as those of males. Finally, females mated to long-tailed (sexually attractive) males decreased their reproductive success the following year more than did females mated to short-tailed males, possibly owing to differential parental effort causing a deterioration of their condition. **Key words:** external tail feathers, life history, reproductive success, tail length manipulation, tradeoffs between life history and sexual selection. [*Behav Ecol* 14:451–456 (2003)]

Sexual selection (i.e., any phenotypic variation nonrandomly related to variation in mating success) often explains the presence of apparently nonadaptive traits in many animal species (Darwin, 1871). Secondary sexual characters might be detrimental in terms of survival, but if they confer mating advantages, they could pass to the next generation. Typical examples of sexually selected traits are the exaggerated long male tails of many birds (Andersson, 1994). Experimental manipulations of tail length proved two decades ago that long tails in male long-tailed widowbirds (*Euplectes progne*) conferred mating advantages (Andersson, 1982). Another bird species with long tails and intensively studied is the barn swallow (*Hirundo rustica*), but in this case, the function of long tail streamers has been the subject of a long debate (see Barbosa and Møller, 1999; Evans, 1998; Evans and Thomas, 1997; Hedenström, 1995; Hedenström and Møller, 1999; Møller et al., 1998; Thomas and Rowe, 1997). Some researchers support the hypothesis that the external tail feathers may have been elongated exclusively by means of natural selection processes, because long tails may provide some advantages in flight performance (Norberg, 1994). On the other hand, much evidence has been accumulated that supports the hypothesis that sexual selection has played and still plays an important role in the evolution and maintenance of external tail feathers in male barn swallows (Møller, 1988; for a review, see Møller et al., 1998). Some authors consider

that both natural and sexual selection could have contributed to the elongation of external tail feathers (Buchanan and Evans, 2000; Rowe et al., 2001).

Most studies trying to identify the function of external tail feathers in the barn swallow have focused on males; much less attention has been paid to females. Until very recently, the study of presumed ornamental traits in females of avian species has been a neglected topic (for a review, see Amundsen, 2000). In barn swallows, females also have considerably long tails, longer than those of juveniles of the two sexes, but significantly shorter than males (Cramp, 1988; Møller, 1994). There is no agreement if tail length in female barn swallows is the optimum according to natural selection (Hedenström and Møller, 1999; Møller et al., 1998), or if it has been elongated beyond that optimum by sexual selection (Buchanan and Evans, 2000; Rowe et al., 2001). An observational study with large sample size (Møller, 1993) suggested that tail length in female barn swallows could be considered a sexual ornament because it reliably reflected female reproductive potential, and because males mated to long-tailed females achieved a selective advantage. However, an experimental study in a different population (Cuervo et al., 1996a) did not find any evidence for tail length in females being an ornament. Cuervo et al. (1996a) assumed that tails in female barn swallows were longer than the optimum according to natural selection, because females had longer tails than juveniles. Tail elongation in females could have been a consequence of strong directional female preference for long-tailed males if there is a strong genetic correlation between the character in the two sexes (correlated response hypothesis; Lande, 1980; Lande and Arnold, 1985). Another possibility is that long tails also confer mating advantages to females (ornament hypothesis). If this is the case, long tails in females could reflect either reproductive or

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parenting ability (Hoelzer, 1989), genetic quality (Iwasa et al., 1991; Zahavi, 1975), or simple attractiveness (Fisher, 1930; Pomiankowski et al., 1991). Cuervo et al. (1996a) manipulated the length of external tail feathers, but they did not find any evidence that male mating preferences depended on female tail length, thus supporting the correlated response hypothesis for the existence of exaggerated long tails in females. Moreover, they found that neither experimental treatment (elongation or shortening of external tail feathers) nor original female tail length previous to the treatment had a significant effect on a number of reproductive variables: start of laying, offspring provisioning, total number of eggs, and total number of fledglings.

In an attempt to understand the function of the external tail feathers in female barn swallows, as well as the evolutionary forces that have driven their evolution, Cuervo et al. (1996b) also calculated daily energy expenditure in the females with experimentally manipulated tail length. They used the doubly labeled water technique that measures respiration rates, specifically carbon dioxide production, and allows calculation of estimates of energy expenditure (Bryant, 1989). If tail length is optimal according to natural selection, any tail length modification will impair flight performance and will cause either a change in behavior or an increase in energy expenditure. On the other hand, if tail feathers have been elongated by sexual selection beyond the optimum according to natural selection, experimental elongation of tails will also impair flight efficiency. However, experimental shortening might reduce tails to a length closer to the natural selection optimum, and flight performance would then improve. Cuervo et al. (1996b) found no significant evidence for behavioral changes in the birds involved in the experiment. Surprisingly, experimental treatment had no significant consequences on energy expenditure, although both natural and sexual selection hypotheses predicted some effect of tail length manipulation on flight performance and on energetic costs. Females of other avian species have also shown no change in energy expenditure owing to flight costs (Moreno et al., 1999). Probably, assessing energy expenditure during a short period of time (24 h) was not the most appropriate method to detect costs of tail length manipulation.

Given that no significant differences were found among the three experimental groups of female barn swallows with very different tail length, can we conclude that tail length manipulation in females does not have any effect on flight performance? There is an important factor that we have not considered, because barn swallows may be able to adjust their effort in the short term. However, if tail length manipulation impairs flight performance, and barn swallows adjust their effort to balance flight deficiencies, this extra effort will have long-term consequences. It has been already shown in male barn swallows that tail length manipulation had a long-term effect, because survival decreased with tail elongation and increased with tail shortening (Møller and de Lope, 1994). This finding supports the assumptions that (1) long tails are costly in males and (2) tail length manipulation may have long-term effects. Most remarkable, survival cost of tail length manipulation was related to original tail length, with naturally long-tailed males being better able to survive tail elongation, and naturally short-tailed males benefiting more from tail shortening (Møller and de Lope, 1994). In another study, male barn swallows had tail length experimentally manipulated, and a number of fitness components were examined the following year (Møller, 1989). Males with elongated tails produced significantly fewer fledglings the following year, and some other traits also showed significant deterioration. No significant differences were found between males with shortened and unmanipulated tails.

As we found no significant effect of tail length manipulation on behavior or reproductive success of female barn swallows in the year when the experiment took place (Cuervo et al., 1996a,b), we have now studied exactly the same individuals the following year. Our aim was to assess possible long-term consequences of the manipulation. We presumed that survival, tail length, or reproductive performance might have been affected. In case of finding an effect of tail manipulation, we would be able also to better understand the forces that may have affected the evolution of the external tail feathers in female barn swallows.

METHODS

Barn swallows are small insectivorous passerines (approximately 20 g) that feed on the wing. Sexual dimorphism is slight, with the exception of the external tail feathers, which are generally longer in males than in females. They are mostly socially monogamous, build nests out of mud and vegetal fragments associated with human constructions, and may have two or even three clutches per year. Populations breeding in Europe winter in Africa south of Sahara, and arrive at the breeding grounds between February and April, depending on latitude. Tail feathers are molted once every year in the winter quarters (for more information on the species, see Cramp, 1988; Møller, 1994). This study was carried out at Badajoz, southwestern Spain, in 1994 and 1995. The field area consists of agricultural land with scattered groups of trees (de Lope, 1983). Swallows bred in farm rooms, getting permanent access through open doors and windows. Swallows included in this study bred colonially in three farms located less than 5 km apart. Morphological measurements or reproductive performance of female swallows did not differ among farms (Cuervo et al., 1996a), and consequently, we pooled the data from the three farms for subsequent analyses.

In 1994 and 1995, swallows were caught early after arrival to the breeding area by using mist nets at doors and windows at dawn. Every individual was measured and provided with a numbered metal ring and a unique color combination of plastic rings. Measurements included both right and left external tail feather length, and the mean of the two feathers was considered the length for that character. Every nest was visited at least once a week throughout the breeding season to determine parent identity, date of laying, number of eggs, and number of nestlings. In 1994 all female swallows, when captured the first time, were randomly assigned to one of three experimental treatments: shortened, elongated, or unmanipulated external tail feathers. External rectrices were shortened by cutting a 20-mm-long piece 10 mm from the base of the feather and gluing back the apical part to the original base using cyanoacrylate super glue. For elongation, the feathers were cut 10 mm from the base, and the 20 mm long piece of feather from the shortened group was glued between the apical and the basal pieces. In both treatments, junctions were strengthened by inserting a small piece (approximately 2 mm long) of fine entomological pin into the pulp cavity of the rachis. Females with unmanipulated tails were captured and measured in the same manner as the others. We did not include a second control group in the experiment, cutting and gluing back the feather without change of length, because previous studies had shown that treatment itself had no effect (Møller, 1988, 1992). Although shortened feathers had one junction and elongated feathers had two, we considered the effect of another piece of pin minute and negligible, in agreement with other authors (Smith and Montgomerie, 1991). Only females captured before 27 March were included in the analyses, because we did not manipulate tail length of individuals that arrived late to the breeding area.

Barn swallows show high breeding philopatry (Cramp, 1988; Glutz von Blotzheim and Bauer, 1985), and individuals breeding in 1994 but absent in 1995 were considered to be dead. In other words, we estimated survival from the return rates to the breeding area, as in previous studies (Møller, 1994; Møller and de Lope, 1999). Less than 1% of adults have ever returned 1 year without having been captured the previous year, a result based on more than 1000 adults recaptured (de Lope F, Szép T, and Møller AP, unpublished data). This ensures that our assumption does not cause any important bias in the results. Although we do not know the exact date each individual arrived at the breeding area, we assume that it is highly related to the date of first capture, because between mid February and the end of March all individuals were captured at least every week. We determined the number of nestlings when they were ringed, 12–14 days old. We assume that this number reflects the number of fledglings, because nestling mortality is very rare among nestlings of that age (chicks leave the nest when 3 weeks old).

Statistical analyses were performed according to Sokal and Rohlf (1981) and Siegel and Castellan (1988). A logistic regression (Hosmer and Lemeshow, 1989) was used to test if experimental treatment had a significant effect on female survival. Tail length and dates were $\log_{10}$ -transformed before parametric analyses. Total number of eggs or nestlings were considered as ordinal discrete variables and were analyzed using nonparametric statistical tests. All statistical tests were two-tailed, and the level for significance was .05.

RESULTS

In 1994 we included 48 female barn swallows in the experiment: 15 with elongated tails, 16 with shortened tails, and 17 unmanipulated. From these 48 individuals, only 27 survived to the following year, nine for each experimental treatment. Two of the females alive in 1995 did not breed, however. Proportion of ages in 1994 (1 year old/more than 1 year old) for the 27 surviving females according to treatment was as follows: shortened, two to seven; unmanipulated, three to six; and elongated, one to eight. These proportions do not differ significantly from one another (G test, $G_{adj} = 1.19$, $df = 2$, $p = .57$).

A multiple logistic regression was used to analyze if experimental treatment had an effect on female survival while controlling for the possible effect of original tail length of females in 1994 and male tail length in 1994. None of these variables showed a significant effect on female survival (final value = 30.92, $\chi^2 = 3.95$, $df = 3$, $p = .27$; in all three partial effects, $-.85 \leq t_{44} \leq 1.70$, $p \geq .10$). It is important to include male tail length in the analysis because female reproductive effort depends on the degree of ornamentation of their mates (de Lope and Møller, 1993), and tail length is an ornamental trait in males (Møller, 1988). We repeated the analysis, including in the model the quadratic term of male and female tail length, in order to test if the relationship was curvilinear, but the result was qualitatively similar.

Female tails were longer in 1995 (mean $\pm$ SE = 86.41 ± 1.00 mm, $n = 27$) than in 1994 (mean $\pm$ SE = 85.47 ± 1.09 mm, $n = 27$; paired t test: $t = -2.91$, $df = 26$, $p = .0074$). Tail lengthening did not differ between 1-year-old (mean $\pm$ SE = 0.29 ± 0.75 mm) and more than 1-year-old females (mean $\pm$ SE = 1.12 ± 0.36 mm; t test: $t = -1.07$, $n_1 = 6$, $n_2 = 21$, $p = .30$). This result is not completely in accordance with previous observations in a different population in which female swallows only increased significantly tail length from the first to the second year of life (Møller, 1991). To analyze the possible effect of experimental treatment on female tail length the following year, we did an ANCOVA with female tail

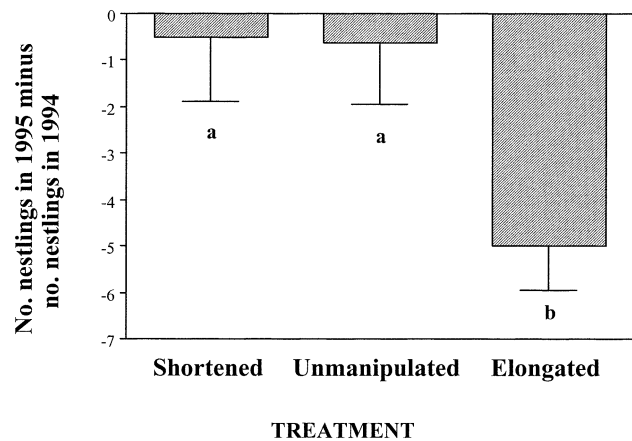


Figure 1

Mean ($\pm$ SE) total number of nestlings in 1995 minus total number in 1994 produced by each female barn swallow for the three experimental treatments: shortened, unmanipulated, and elongated external tail feathers. Different letters mean that the difference is statistically significant ($p < .05$). Females with experimentally elongated tails decreased the number of nestlings the following year compared with that of females with shortened or unmanipulated tails.

length in 1995 as the dependent variable, female tail length in 1994 as the covariate, and experimental treatment as the grouping variable. Although tail length in 1995 was closely related to tail length in 1994 ($F = 288.18$, $df = 1, 23$, $p < .001$), the effect of the treatment did not reach significance ($F = 2.75$, $df = 2, 23$, $p = .085$). Adding male tail length in 1994 to the model gave qualitatively similar results.

To compare phenology of reproduction among experimental groups and between years, we used the date of laying of the first egg. In 1995 females delayed the beginning of reproduction in relation to 1994 (paired t test: $t = -3.08$, $df = 24$, $p = .0052$). By using ANCOVA, we found that breeding dates in 1995 were related to breeding dates in 1994 ($F = 28.06$, $df = 1, 21$, $p < .001$) but were not related to experimental treatment ($F = .22$, $df = 2, 21$, $p = .81$). Adding male tail length in 1994 to the model gave qualitatively similar results.

Since we cannot consider total number of eggs laid during the breeding season or total number of nestlings as continuous variables, we cannot use parametric tests as done above. We have simply compared the difference in number of eggs laid by each female in 1995 and 1994 among experimental groups. Females laid fewer eggs in 1995 than in 1994 (Wilcoxon signed-rank test: $n = 25$, $z = 3.30$, $p = .0010$), but the decrease in number of eggs did not differ significantly among groups with different tail treatment (Kruskal-Wallis test: $KW = 1.27$, $n_1 = n_2 = 8$, $n_3 = 9$, $p = .53$). Total number of nestlings produced by each female was also smaller in 1995 than in 1994 (Wilcoxon signed-rank test: $n = 25$, $z = 2.32$, $p = .020$), on average 2.56 nestlings less in the whole season. However, the decrease in the total number of nestlings (1995 minus 1994) differed significantly among experimental groups (Kruskal-Wallis test: $KW = 7.59$, $n_1 = n_2 = 8$, $n_3 = 9$, $p = .023$). More specifically, females with elongated tails had a reduced number of nestlings the following year compared with that of females with shortened (Mann-Whitney test: $U = 60.5$, $n_1 = 8$, $n_2 = 9$, $p = .017$) or unmanipulated tails ($U = 59.5$, $n_1 = 8$, $n_2 = 9$, $p = .022$). We found no significant difference in number of nestlings between females with shortened and unmanipulated tails ($U = 35.5$, $n_1 = n_2 = 8$, $p = .71$) (Figure 1).

In the previous analyses concerning variation between years in number of eggs and nestlings, we have not controlled for male tail length, an important character that could influence

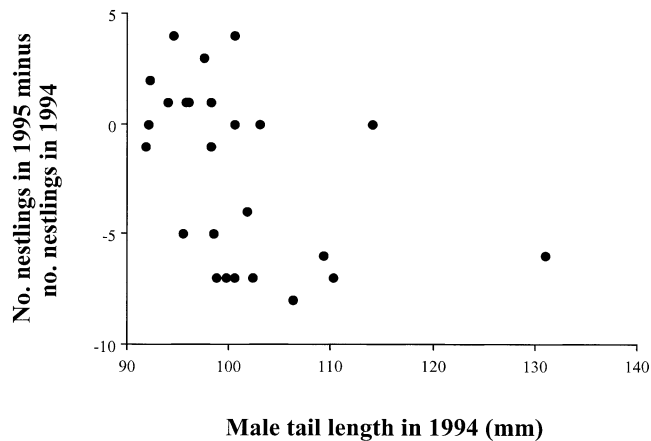


Figure 2

Relationship between total number of nestlings in 1995 minus total number in 1994 and tail length of their mate in 1994 for each female barn swallow involved in the experiment. Females that most notably reduced nestling production in 1995 in relation to 1994 were the ones mated to long-tailed males in 1994.

female reproductive effort (de Lope and Møller, 1993). Therefore, we have explored if male tail length was related to the decrease in reproductive success experienced by females in 1995 relative to 1994. Variation in total number of eggs was not significantly related to tail length of males in 1994 (Kendall rank-order correlation: $T = -.035$, $n = 25$, $p = .81$) or in 1995 ($T = -.014$, $n = 25$, $p = .92$). Variation in total number of nestlings was not significantly related to tail length of males in 1995 ($T = .021$, $n = 25$, $p = .88$), but we found a statistically significant negative relationship between the decrease in number of nestlings and male tail length in 1994 ($T = -.365$, $n = 25$, $p = .010$). That is, females paired to long-tailed males in 1994 had decreased production of nestlings the following year compared with that of females mated to short-tailed males (Figure 2). The significant differences among experimental groups in the decrease of total number of nestlings may be influenced by original tail length of males. Therefore, we tested whether male tail length differed among treatments in 1995 and 1994. Differences in male tail length among experimental groups were far from significant in 1995 (Kruskal-Wallis test: $KW = 0.26$, $n_1 = n_2 = 8$, $n_3 = 9$, $p = .88$) and 1994 ($KW = 0.63$, $n_1 = n_2 = 8$, $n_3 = 9$, $p = .73$; we have only included males whose females bred also in 1995). Thus, we can conclude that the relationship between decrease in number of nestlings and male tail length in 1994 was not confounded by treatment.

DISCUSSION

Previous studies have shown that experimental tail length manipulation in female barn swallows at the beginning of a breeding season caused no significant change in female parental behavior and reproductive success during that breeding season (Cuervo et al., 1996a,b). However, we have found some effects of the manipulation the following year, the so-called long-term effects, in contrast to the short-term effects during the same year. Females whose external tail feathers were experimentally elongated in 1994 produced less fledglings in the breeding season of 1995 than did females with shortened or unmanipulated tails. This result suggests that tail elongation in female barn swallows caused flight deficiencies and had, indeed, a detrimental long-term effect. This implies that female barn swallows have the ability to adjust parental

investment. They can balance imposed handicaps, maybe by making an extra effort, and continue for a certain time with normal levels of parental investment. However, present extra effort will lead to a future cost. We found a convincing reason why female barn swallows do not have longer tail feathers: Although mating advantages of long-tailed females have never been confirmed (Cuervo et al., 1996a), here we show detrimental effects of long tails in terms of decreased reproductive success. For long tail feathers in males, both advantages (Møller, 1988, 1992; Saino et al., 1997) and disadvantages (Møller and de Lope, 1994; Møller et al., 1995) have been found. Differential selective forces on male and female barn swallows may thus have given rise to the current sexual dimorphism in tail length. Moreover, reduced reproductive success owing to female tail elongation could be also interpreted as a selective force weakening sexual selection for tail lengthening in females. Interestingly, male tail length would be also affected if, as it seems to be the case, there is a significant genetic correlation between the sexes for that character (Møller, 1993). The trade-off between ornamentation and parental investment has been largely discussed in the literature (Fitzpatrick et al., 1995), and some theoretical models have shown that expression and honesty of ornaments will depend on marginal fitness gains of advertisement effort (Kokko, 1998).

It is interesting to notice that tail elongation had significant effects on reproductive success the following year, but not on survival. Similar experiments in male barn swallows have found that tail elongation diminished survival probability (Møller and de Lope, 1994). Even if tail elongation had an effect on female survival that we have not detected, our results suggest that reproductive success is more sensitive to small changes in condition than is survival. Moreover, barn swallows may live for 5 years or longer (Møller and de Lope, 1999), and there is probably a trade-off between current effort in reproduction and survival prospects (Saino et al., 1999). Barn swallows should have the ability to maximize reproductive effort while not seriously compromising survival. We have also found that experimental tail length manipulation in 1994 did not significantly affect date of laying of the first egg or number of eggs laid during 1995. This implies that differences in number of fledglings among treatments were not caused by differences in phenology or in number of eggs. Maybe poor condition is only expressed in the most energy demanding activities. Provisioning of young is generally considered to be the most energy demanding activity of parental care (Clutton-Brock, 1990; Winkler and Wilkinson, 1988), which could explain why there was no significant effect of experimental treatment on number of eggs, but the effect was notable for number of fledglings.

Both natural and sexual selection hypotheses for the evolution of tail length in female barn swallows predict that experimental elongation will be costly (see Introduction), as we have found. However, only experimental shortening can distinguish between the two hypotheses. According to the natural selection hypothesis, individuals with shortened tails will suffer a cost because tail length has been displaced from the optimum, what entails flight deficiencies. According to the sexual selection hypothesis, the tail has been elongated by sexual selection beyond the natural selection optimum, and individuals with shortened tails will enjoy a benefit in terms of flight performance, because shortening will bring tail length nearer to that optimum. In this study, as found in previous studies (Cuervo et al., 1996a,b), females with shortened or unmanipulated tails showed no significant differences in a number of variables. This result does not support any of the hypotheses. The nonsignificant effect of experimental tail shortening could be explained in at least two ways. First, we

recognize that the number of females involved in the experiment is rather small, and very strong effects would be necessary to show significant differences. A total of 48 females were initially included in the experiment, but only 25 survived to the following year and bred, which implies less than 10 individuals per experimental treatment. With such a small sample size, nonsignificance does not necessarily imply no treatment effect (e.g., nestling comparison between females with shortened and unmanipulated tails, power = 0.07, $w = 0.09$ [small effect size sensu, Cohen, 1988], although tail length comparison between the same two groups of females, power = 0.24, $w = 0.30$ [intermediate effect size sensu, Cohen, 1988]). We recognize that conclusions based on such a small sample size should be considered with caution. Second, recent studies have suggested that tail length both in male and female barn swallows might be 10–12 mm longer than the natural selection optimum owing to sexual selection (Buchanan and Evans, 2000; Rowe et al., 2001). If this is correct, our experimental shortening by 20 mm would have resulted in tails 8–10 mm shorter than the natural selection optimum. On the other hand, unmanipulated birds would have tails 10–12 mm longer than the optimum. With such a similar difference in tail length for the two groups of females in relation to the optimal tail length, a similar effect of the two treatments would not be surprising. Interestingly, in a study in which male tail length was manipulated in a similar manner and fitness components were examined the following year, tail lengthening had strong effects on male fitness, but no significant differences were found between males with shortened and unmanipulated tails (Møller, 1989). Effects of tail elongation and shortening for males were quite similar to the effects that we have found for females.

A major result of our study is the negative relationship between male tail length and the future reproductive success of their mates. It is known that female barn swallows adjust their reproductive effort to the attractiveness of their mates. Females mated to long-tailed males, i.e., attractive males, increase their parental investment (de Lope and Møller, 1993). Another nonexclusive explanation could be that long tails impair flight performance, and long-tailed males cannot obtain the same quantity or quality of food (Møller et al., 1995). In that case, females would have to compensate deficiencies of their mates in provisioning of young. However, such compensation does not explain why females mated to attractive males also more often produce a second clutch, than do females mated to short-tailed males, and thereby repeat their differential parental investment (de Lope and Møller, 1993). Differential female investment in reproduction will lead to deterioration in condition. Extra reproductive costs 1 year will be paid for the following year with a decrease in reproductive success. This tradeoff between the allocation of resources to current or future reproductive effort is a cornerstone of life-history theory (Höglund and Sheldon, 1998; Reznick et al., 2000). In general, the findings of this study emphasize the need for long-term studies (the closer to the lifetime of the organism, the better) when attempting to elucidate the effect of a handicap on parental investment. Apparently, absent short-term effects may be owing to compensation for the detrimental effects of handicaps, but it does not imply that they are not important in terms of survival or lifetime reproductive success. Therefore, short-term studies may provide misleading conclusions.

To sum up, in this study we have found a long-term detrimental effect of experimental tail elongation in female barn swallows. Females with elongated external rectrices produced less offspring during the breeding season the following year than did females with shortened or unmanipulated tails. This result suggests that tail elongation caused

flight deficiencies that affected condition and eventually reduced reproductive success. The finding of long-term effects but no significant short-term effects (Cuervo et al., 1996a,b) for female tail elongation suggests that female barn swallows have the ability to adjust parental investment. Detrimental effects of long tails in females in terms of low reproductive success might explain why females have shorter tails than do males in this species. Finally, females mated to long-tailed males decreased their reproductive success the following year, possibly owing to differential parental investment that caused deterioration in female condition.

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REFERENCES

- Amundsen T, 2000. Why are female birds ornamented? *Trends Ecol Evol* 15:149–155.
- Andersson M, 1982. Female choice selects for extreme tail length in a widowbird. *Nature* 299:818–820.
- Andersson M, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Barbosa A, Møller AP, 1999. Sexual selection and tail streamers in the barn swallow: appropriate tests of the function of size-dimorphic long tails. *Behav Ecol* 10:112–114.
- Bryant DM, 1989. Determination of respiration rates of free-living animals by the double-labelling technique. In: *Toward a more exact ecology* (Grubb PJ, Whittaker JB, eds). Oxford: Blackwell; 85–109.
- Buchanan KL, Evans MR, 2000. The effect of tail streamer length on aerodynamic performance in the barn swallow. *Behav Ecol* 11: 228–238.
- Clutton-Brock TH, 1990. The evolution of parental care. Princeton, New Jersey: Princeton University Press.
- Cohen J, 1988. Statistical power analysis for the behavioral sciences, 2nd ed. Hillsdale, New Jersey: Erlbaum Associates.
- Cramp S (ed), 1988. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic, vol. 5. Oxford: Oxford University Press; 262–278.
- Cuervo JJ, de Lope F, Møller AP, 1996a. The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behav Ecol* 7:132–136.
- Cuervo JJ, de Lope F, Møller AP, Moreno J, 1996b. Energetic cost of tail streamers in the barn swallow (*Hirundo rustica*). *Oecologia* 108:252–258.
- Darwin C, 1871. The descent of man, and selection in relation to sex. London: John Murray.
- de Lope F, 1983. La avifauna de las Vegas Bajas del Guadiana. *Doñana Acta Vert* 10:91–121.
- de Lope F, Møller AP, 1993. Female reproductive effort depends on the degree of ornamentation of their mates. *Evolution* 47:1152–1160.
- Evans MR, 1998. Selection on swallow tail streamers. *Nature* 394: 233–234.
- Evans MR, Thomas ALR, 1997. Testing the functional significance of tail streamers. *Proc R Soc Lond B* 264:211–217.
- Fisher RA, 1930. The genetical theory of natural selection. Oxford: Clarendon Press.
- Fitzpatrick S, Berglund A, Rosenqvist G, 1995. Ornaments or offspring: costs to reproductive success restrict sexual selection processes. *Biol J Linn Soc* 55:251–260.
- Glutz von Blotzheim UN, Bauer KM (eds), 1985. Handbuch der vögel mitteleuropas, vol 10. Wiesbaden, Germany: AULA.
- Hedenström A, 1995. Swallows unhandicapped by long tails? *Trends Ecol Evol* 10:140–141.
- Hedenström A, Møller AP, 1999. Length of tail streamers in barn swallows. *Nature* 397:115.
- Hoelzer GA, 1989. The good parent process of sexual selection. *Anim Behav* 38:1067–1078.
- Höglund J, Sheldon BC, 1998. The cost of reproduction and sexual selection. *Oikos* 83:478–483.

- Hosmer DW, Lemeshow S, 1989. Applied logistic regression. New York: Wiley.
- Iwasa Y, Pomiankowski A, Nee S, 1991. The evolution of costly mate preferences, II: the "handicap principle." *Evolution* 45:1431–1442.
- Kokko H, 1998. Should advertising parental care be honest? *Proc R Soc Lond B* 265:1871–1878.
- Lande R, 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution* 34:292–305.
- Lande R, Arnold SJ, 1985. Evolution of mating preferences and sexual dimorphism. *J Theor Biol* 117:651–664.
- Møller AP, 1988. Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* 332:640–642.
- Møller AP, 1989. Viability costs of male tail ornaments in a swallow. *Nature* 339:132–135.
- Møller AP, 1991. Sexual selection in the monogamous barn swallow (*Hirundo rustica*), I: determinants of tail ornament size. *Evolution* 45:1823–1836.
- Møller AP, 1992. Female swallow preference for symmetrical male sexual ornaments. *Nature* 357:238–240.
- Møller AP, 1993. Sexual selection in the barn swallow *Hirundo rustica*, III: female tail ornaments. *Evolution* 47:417–431.
- Møller AP, 1994. Sexual selection and the barn swallow. Oxford: Oxford University Press.
- Møller AP, Barbosa A, Cuervo JJ, de Lope F, Merino S, Saino N, 1998. Sexual selection and tail streamers in the barn swallow. *Proc R Soc Lond B* 265:409–414.
- Møller AP, de Lope F, 1994. Differential costs of a secondary sexual character: an experimental test of the handicap principle. *Evolution* 48:1676–1683.
- Møller AP, de Lope F, 1999. Senescence in short-lived migratory bird: age-dependent morphology, migration, reproduction and parasitism. *J Anim Ecol* 68:163–171.
- Møller AP, de Lope F, López-Caballero JM, 1995. Foraging costs of a tail ornament: experimental evidence from two populations of barn swallows *Hirundo rustica* with different degrees of sexual size dimorphism. *Behav Ecol Sociobiol* 37:289–295.
- Moreno J, Merino S, Potti J, de León A, Rodríguez R, 1999. Maternal energy expenditure does not change with flight costs or food availability in the pied flycatcher (*Ficedula hypoleuca*): costs and benefits for nestlings. *Behav Ecol Sociobiol* 46:244–251.
- Norberg RÅ, 1994. Swallow tail streamer is a mechanical device for self-deflection of tail leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proc R Soc Lond B* 257:227–233.
- Pomiankowski A, Iwasa Y, Nee S, 1991. The evolution of costly mate preferences, I: Fisher and biased mutation. *Evolution* 45:1422–1430.
- Reznick D, Nunney L, Tessler A, 2000. Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol Evol* 15:421–425.
- Rowe LV, Evans MR, Buchanan KL, 2001. The function and evolution of the tail streamer in hirundines. *Behav Ecol* 12:157–163.
- Saino N, Calza S, Ninni P, Møller AP, 1999. Barn swallows trade survival against offspring condition and immunocompetence. *J Anim Ecol* 68:999–1009.
- Saino N, Primmer C, Ellegren H, Møller AP, 1997. An experimental study of paternity and tail ornamentation in the barn swallow (*Hirundo rustica*). *Evolution* 51:562–570.
- Siegel S, Castellan NJ Jr, 1988. Nonparametric statistics for the behavioral sciences, 2nd ed. New York: McGraw-Hill.
- Smith HG, Montgomerie R, 1991. Sexual selection and the tail ornaments of North American barn swallows. *Behav Ecol Sociobiol* 28:195–201.
- Sokal RR, Rohlf FJ, 1981. Biometry, 2nd ed. San Francisco: Freeman.
- Thomas ALR, Rowe L, 1997. Experimental tests on tail elongation and sexual selection in swallows (*Hirundo rustica*) do not affect the tail streamer and cannot test its function. *Behav Ecol* 8:580–581.
- Winkler DW, Wilkinson GS, 1988. Parental effort in birds and mammals: theory and measurement. Oxford Surv Evol Biol 5:185–214.
- Zahavi A, 1975. Mate selection: a selection for a handicap. *J Theor Biol* 67:205–214.