



Sexual selection and tail streamers in the barn swallow

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The functional significance of elongated, narrow tips of the tail feathers of certain birds, so-called tail streamers, has recently been discussed from an aerodynamic point of view, and the effects of sexual selection on such traits have been questioned. We review our long-term field studies using observational and experimental approaches to investigate natural and sexual selection in the barn swallow, *Hirundo rustica*, which has sexually size-dimorphic outermost tail feathers. Experimental manipulation of the length of the outermost tail feathers has demonstrated sexual selection advantages of tail elongation and disadvantages of tail shortening, with opposite effects for natural selection in terms of foraging efficiency, haematocrit and survival. These findings are contrary to the prediction of a general deterioration from both shortening and elongation, if the tail trait was determined solely by its effects on aerodynamic efficiency and flight manoeuvrability. Patterns of sexual selection in manipulated birds conform with patterns in unmanipulated birds, and selection differentials for different components of sexual selection in manipulated birds are strongly positively correlated with differentials in unmanipulated birds. Age and sex differences in tail length, and geographical patterns of sexual size dimorphism, are also consistent with sexual selection theory, but inconsistent with a purely natural selection advantage of long outermost tail feathers in male barn swallows.

Keywords: aerodynamics; costs of sexual selection; *Hirundo rustica*; reliable signalling; tail manipulation

1. INTRODUCTION

Extravagant feather ornaments, such as long tails in male birds, have played a pivotal role in the study of sexual selection since Darwin (1871) first introduced the subject. Numerous observations and experiments have demonstrated that females indeed prefer males with longer feather ornaments in the long-tailed widowbird, *Euplectes progne* (Andersson 1982), and a large number of other species, and that female choice rather than male–male competition maintains exaggerated feather traits in male birds (reviewed in Andersson 1994). The size of extravagant tail feathers presumably exceeds the optimum under natural selection, which is the phenotype in females, and the costs of ornamentation are thus balanced by the benefits of sexual selection. Secondary sexual characters such as long tails are therefore shaped by both natural and sexual selection. Secondary sexual characters may also have directly beneficial effects due to natural selection. For example, cockerels use their spurs to fight with other males for access to females, but they also use these in attempts to avoid being eaten by a predator. Similarly, if bright coloration is a reliable signal of condition, this should also be the case for specialist

predators that should differentially select less adorned males as prey, simply because they are easier to catch. These benefits of natural selection will tend to reduce the costs of the exaggeration evolved as a result of sexual selection, although it seems unlikely that such benefits would be large. If they were large, we should expect both males and females to have exaggerated characters.

Recently, Norberg (1994) suggested that the exaggerated tail streamers of male barn swallows, *Hirundo rustica*, may provide individuals with a natural selection advantage. If this mechanism is of general importance, we should expect natural rather than sexual selection to account for the maintenance of exaggerated tail feathers in species with forked tails. His idea is that the aerodynamic function of tail streamers is to increase lift generated by the tail through aeroelastic properties translated from the distal parts of the feather, causing a rotation in their sockets. Hence, a natural selection advantage of long tail streamers in males would arise. We would like to stress that this is a hypothetical mechanism with an importance of unknown magnitude. Hedenström (1995) correctly pointed out that the longer tail in male as compared to female barn swallows must be accounted for by sexual selection. Therefore, the mechanism proposed by Norberg has several gaps. The functional relationship between streamer length and the degree of deflection of the leading edge of the tail remains to be determined.

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Therefore, the minimum streamer length necessary to obtain the maximum deflection, i.e. feather rotation, remains unknown. If Norberg's mechanism is due to long streamers projecting outside the maximum tail span, when the tail is spread as in turning flight, another question arises. Why do females have streamers of a similar shape to those of males if streamers in most females do not project outside the maximum tail span in a spread tail? Could the morphology of female streamers be sufficient to cause rotation of feathers, and therefore an optimal morphology? Norberg's (1994) paper does not answer these questions, although he proposed several possible modifications in feather morphology to compensate for the possible costs of excessively long streamers. His proposals remain to be tested and the magnitude of any functional relationship between streamer length and feather rotation remains to be explored.

There is evidence favouring the hypothesis that female streamers are close to the aerodynamically optimal phenotype. A study of geographical variation of tail morphology in female barn swallows showed a similar shape of female tails in all populations, with streamers not projected outside the maximum tail span. Furthermore, although both outermost and central tail feathers demonstrated clinal latitudinal variation, this variation was isometric, giving rise to an aerodynamically optimal morphology in females at all latitudes (A. Barbosa and A. P. Møller, unpublished data). Evans & Thomas (1997) have taken Norberg's line of reasoning one step further by stating that if the tail streamer is a mechanical device enhancing aerodynamic efficiency and flight manoeuvrability, then any manipulation of the length of the tail (either shortening or elongation) should result in increased costs for aerodynamic reasons, and that only manipulation of the streamer itself could resolve whether natural rather than sexual selection accounted for exaggeration of this character. Different parts of the outermost tail feather are correlated with each other, and experimental manipulation of both basal parts of the feather and the streamer causes a change in the ratio between the length of the basal part of the feather and the streamer. The lack of quantification of the relationship between streamer length, length of the basal part of the feather, and the magnitude of the deflecting mechanism make statements about the superiority of any particular kind of manipulation premature.

Contrary to Evans & Thomas (1997), we are prepared to argue that our current knowledge of the selection pressures affecting tail length and shape in the barn swallow is entirely consistent with the exaggerated part of the trait in males being subject to sexual selection. Actually, the arguments presented by Evans & Thomas (1997) suffer from a number of omissions that need to be addressed. The aims of this paper are to pinpoint these omissions and present the evidence for natural versus sexual selection affecting the expression of the outermost tail feathers in the barn swallow.

The barn swallow is a sexually size-dimorphic, aerial-insectivorous passerine in which males attract mates by displaying their exaggerated, outermost tail feathers (Møller 1994a). The tail of the barn swallow is forked, with the outermost feathers being considerably longer than the central ones. Juveniles have short, forked tails of

similar length in both sexes, while adult females have tails that are intermediate in length between those of juveniles and adult males (Møller 1994a). There is a strongly positive genetic correlation between the sexes for tail length, implying that selection for increased tail length in males will automatically give rise to a correlated response to selection in females, and this can readily account for a slightly elongated tail in females as compared to juveniles (Møller 1993). Although long tails in females are weakly positively correlated with body condition (Møller 1993), they do not confer any mating advantage to females, since females with elongated tails do not mate more quickly than controls or tail-shortened females (Cuervo *et al.* 1996a). This experimental result is consistent with the observation that it is body condition, but not tail length *per se*, which confers a reproductive advantage to males that mate with long-tailed females (Møller 1993, 1994a). We should expect female performance to deteriorate considerably, independent of the direction of tail manipulation, according to the aerodynamic arguments of Evans & Thomas, if the tail streamer in females played a pivotal role in foraging efficiency (Evans & Thomas 1997, p. 213). However, tail manipulation of females had no measurable effect on reproductive performance, offspring condition or feeding rate of chicks (Cuervo *et al.* 1996a), or on field metabolic rate (Cuervo *et al.* 1996b).

Males in a Danish study population have tails that are on average almost one-fifth longer than those of females, and it is this difference that is presumed to be maintained by sexual selection (Møller 1991b). The effects of age on the expression of the secondary sexual character are small, since tail length only increases by 4.8 mm from the first to the second year of life, and not significantly during subsequent years. After correction for the effects of age, the repeatability of tail length among years remains almost identical (Møller 1991b). More than 90% of the variance in male tail length is due to variation among males (Møller 1991b, 1994a).

There is considerable geographical variation in sexual size dimorphism in tail length, increasing from *ca.* 5% in Morocco to more than 25% in northern Scandinavia, almost entirely due to variation in the length of tails in males (Møller 1995). There is no difference in sex ratio of adult breeders between southern Spain, Italy and Denmark, with an excess of males of *ca.* 13% (Møller 1994a; F. de Lope, A. P. Møller and N. Saino, unpublished data). Clinal variation in size dimorphism may be related to increased foraging costs caused by long tails in southern Europe and northern Africa, where high ambient temperatures make capturing insect prey more difficult, especially for extravagantly ornamented males; this has been shown in field experiments (Møller *et al.* 1995a). If long tails were to increase aerodynamic efficiency and flight manoeuvrability, as suggested by Norberg (1994), we might expect the opposite pattern of sexual size dimorphism, since selection for improved aerodynamic performance would be stronger in the southern part of the breeding range.

2. SEXUAL SELECTION ON TAIL LENGTH

Contrary to the statements by Evans & Thomas (1997), there exists extensive observational and experimental

evidence for sexual selection in the barn swallow, which we review here. Hence, the question is not whether natural or sexual selection may have affected the evolution and the maintenance of elongated tail feathers, but the relative importance of the two processes. There is good evidence of genetic variation in tail length in the barn swallow (Møller 1991*b*, 1994*a*), and it would seem most unusual if only one selective force (natural selection) caused an evolutionary response to the exclusion of the other (sexual selection). Natural variation in tail length has been found to affect sexual selection in the barn swallow: male mating success as well as the duration of the pre-mating period are directly related to tail length, even when males are matched with respect to arrival date (Møller 1990*b*, 1994*a*).

Experimental manipulation of the tail length by addition or removal of 20 mm from the basal part of the two outermost tail feathers has been used to investigate whether there is a directional female mate preference for long tail feathers. The magnitude of these manipulations is moderate, and almost all manipulated individuals still have tail lengths within the natural range, due to the rarity of individuals with extreme tail lengths (in Denmark the natural range is 85–146 mm, while the range of manipulated tail lengths has been 82–142 mm). Even the basal parts of manipulated feathers are almost entirely within the natural range of basal tail lengths. Repeated experiments in Denmark, Spain, and Italy have shown clear effects of tail manipulation and original tail length on male mating speed and mating success (Møller 1988; Møller & de Lope 1994). When we initiated these experiments in the 1980s, there was virtually no knowledge of the aerodynamics of tails in birds. Recent developments have partly changed this situation (Thomas 1993; Norberg 1994; Thomas & Balmford 1995). However, the magnitude of these hypothesized effects and their influence on males differing in tail length remain to be determined.

Male success in obtaining extra-pair copulations is also affected by tail length, since females paired with medium- and short-tailed males preferentially have extra-pair copulations with long-tailed males (Møller 1988). Extra-pair copulations and extra-pair paternity are affected both by experimental and natural tail length, with similar effects having been observed in two different populations (Saino *et al.* 1997*d*; Møller & Tegelström 1997).

If the 'Norberg effect' was pivotal in enhancing aerodynamic efficiency and flight manoeuvrability, we would have to expect long-tailed individuals of both sexes to be better foragers. However, long-tailed males provide less parental care than short-tailed ones, both when considering natural and experimental tail length (Møller 1992, 1994*c*; de Lope & Møller 1993). High circulating levels of testosterone in long-tailed males are causally related to reduced male feeding rates, as demonstrated by observations and testosterone implant experiments (Saino & Møller 1995*a*). Hence, females suffer a direct cost as a consequence of being mated to an attractive long-tailed male. While this effect is difficult to reconcile with long-tailed males being aerodynamically more efficient, it makes eminent sense from a sexual selection viewpoint (Møller 1994*a*).

If, for the moment, we assume that the Norberg effect is of overriding importance in shaping tail length in the barn

swallow, there are still two measures of sexual selection which do not rely on aerodynamics. First, the tail feathers of barn swallows have a white spot near their base; a trait that is sexually size-dimorphic, displayed during nuptial flights, and positively correlated with tail length. We used a dyeing experiment to test whether spot size affected sexual selection. Males with randomly treated outermost tail feathers bred later if their tail spots were reduced in size or completely eliminated, as compared to males receiving a sham treatment (Kose 1997). Thus, a colour signal which does not affect aerodynamics is directly involved in sexual selection. Second, barn swallows have a red face consisting of feathers containing carotenoid-based colour (mainly lutein, R. Stradi, personal communication). The intensity of coloration is sexually dimorphic, but also directly related to male tail length (N. Saino, A. Camplani and A. P. Møller, unpublished data). Again, the presence of this colour signal does not affect aerodynamics, although it is involved in sexual selection. Interestingly, carotenoids in the blood act as precursors of components of the immune defence that may be the direct target of female choice of males with a bright red colour.

Choosy females which mate with long-tailed males produce more viable offspring that live for longer than the offspring of short-tailed males, even when controlling for a large number of potentially confounding variables (Møller 1994*b*). Females do not acquire any obvious direct fitness benefits from their mate choice (Møller 1994*a*). Loads of several species of parasites are inversely related to tail length (Møller 1990*a*, 1994*a*; Saino & Møller 1994; Saino *et al.* 1995), and resistance to one mite has been shown by cross-fostering experiments to have a genetic basis (Møller 1990*a*). This resistance is directly related to male tail length. Recent studies of immune function in barn swallows have demonstrated direct correlations between immune function and tail length (Saino *et al.* 1995; Saino & Møller 1996), and at least one measure of immunocompetence has an additive genetic basis, as shown by cross-fostering experiments (Saino *et al.* 1997*a*). Again, these findings are difficult to reconcile with a natural selection advantage of long tails, but they make perfect sense when interpreted in the light of sexual selection.

We have conducted a series of studies on the relationship between testosterone and tail length in the barn swallow. Circulating levels of testosterone are positively correlated with male tail length (Saino & Møller 1995). Interestingly, an anti-testosterone experiment using cyproterone acetate demonstrated that the response to the experimental treatment was inversely related to male tail length, implying that the number of testosterone receptors is positively related to male tail length (N. Saino and A. P. Møller, unpublished manuscript). Tail length and testosterone are both positively related to song rate (Saino & Møller 1995*b*; Galeotti *et al.* 1997; Saino *et al.* 1997*c*). Song parameters correlate with male tail length, and song rate is correlated with immune responses (Saino *et al.* 1997*c*). Furthermore, song rate differentially affects paternity, depending on original tail length; song increases paternity in the male's own nest more for long-tailed than for short-tailed males, which implies a differential female response to male behaviour depending on male phenotype (Møller

et al. 1998). Again, it is difficult to understand the origin and the maintenance of these phenotypic correlations under natural selection, but they are perfectly understandable in terms of sexual selection.

Evans & Thomas (1997) have suggested that experimental manipulation of the base of the outermost tail feathers does not test whether the outermost tail feathers provide a sexual selection advantage. We disagree since we have provided extensive evidence for a sexual selection advantage of long tails, as summarized above. In short, the evidence is extremely strong for sexual selection currently affecting tail length of male barn swallows. We would like to emphasize once more that tail length in our experiments has remained almost exclusively within the natural range of tail length of the birds in our populations. The effects of our manipulations closely mirror patterns also visible to unmanipulated birds. Although the magnitude of sexual selection components in the field experiments is larger than in unmanipulated birds, there is a very strong positive correlation between the two sets of selection differentials (Møller 1994a, p. 112). This proves that our experiments have been relevant and biologically meaningful.

3. COSTS OF LONG TAILS AND SEXUAL SELECTION

We have previously presented a considerable amount of evidence concerning costs of long tail feathers imposed upon male barn swallows. While survival prospects are directly related to male tail length (Møller 1991a), experimental manipulation of tails gave rise to an increase in survival for males with shortened tails, but a reduction in survival for tail-elongated males, and this effect was dependent on original tail length (Møller & de Lope 1994; Saino *et al.* 1997b). These findings are consistent with the expectations from condition-indicator mechanisms of sexual selection (Andersson 1994), but do not support the prediction based on an optimal morphology under natural selection, since then all manipulations should result in a deterioration of performance (Evans & Thomas 1997). The differential survival of different phenotypes could conceivably be caused by differences in flight cost, although an extensive doubly labelled water experiment did not support this hypothesis (Cuervo *et al.* 1996b). Foraging costs of tail manipulation have been demonstrated repeatedly, with tail elongation resulting in smaller, more easily captured insect prey being caught and tail shortening in larger, more agile insect prey being taken (Møller 1989; de Lope & Møller 1993; Møller *et al.* 1995a). The significance of such a foraging cost of long tails is also indirectly supported by physiological cost estimates from haematocrit values. Long-tailed males achieve a larger concentration of erythrocytes as shown by higher haematocrit values than short-tailed males, and this is also the case for experimental, tail-manipulated swallows (Saino *et al.* 1997e,f). High haematocrit values reflect metabolic activity during a period of days to weeks before blood sampling (Carpenter 1975), such as in long distance migrants (Saino *et al.* 1997f), and high haematocrit values imply that long-tailed males have a higher activity level than short-tailed ones; a finding that is difficult to reconcile with supposedly enhanced aerodynamic efficiency and flight manoeuvrability.

Predation costs may also affect the tail trait, and an investigation of adult barn swallows captured by sparrowhawks, *Accipiter nisus*, showed that males were captured more often than expected from random (Møller & Nielsen 1997). These males were taken mainly during mobbing, although males and females mob predators with similar intensity. Male barn swallows captured by sparrowhawks had longer and more asymmetric tails than surviving males (Møller & Nielsen 1997).

A final cost of long tails arises in terms of reduced efficiency of immune function, with tail elongation but not tail shortening being associated with reduced responsiveness to injections with sheep red blood cells (Saino & Møller 1996). Interestingly, when the costs of tails are increased by tail elongation, males with originally long tails are better able to mount an immune response than short-tailed ones (Saino & Møller 1996).

In conclusion, empirical evidence for tail shortening improving survival and foraging negates the predictions derived from the Norberg effect, but is consistent with sexual selection theory. Similarly, empirical evidence for genetically based parasite resistance and immune responsiveness being directly linked to male, but not female, tail length is also difficult to reconcile with the Norberg effect, but can readily be explained in terms of sexual selection theory.

4. ORIGIN OF TAIL STREAMERS

If we were to assume that the Norberg effect might account for the evolution and the maintenance of long tail feathers in the barn swallow, especially males, we would expect it to apply particularly to other species with aerial foraging habits and for which aerodynamic efficiency and flight manoeuvrability are of obvious importance. A comparative study of tail morphology of birds with long and sexually size-dimorphic tails and closely related species with short, sexually size monomorphic tails, respectively, revealed that the long tails of males had evolved much narrower feather tips with feather vanes of more similar width than the tail feathers of males of the closely related short-tailed, size-monomorphic species (A. P. Møller and A. Hedenström, unpublished manuscript). This was the case independent of whether the elongated tail feathers were the outermost feathers, as in species with forked tails (like the barn swallow), or the innermost tail feathers as in species with pintails and graduated tails. This was also the case independent of foraging mode (aerial versus perching or fossorial). These findings suggest that the evolution of a narrow feather-tip with vanes of similar width is a mechanism for reducing the cost of a long tail, since the drag of a feather is directly proportional to its width (Møller *et al.* 1995b; A. P. Møller and A. Hedenström, unpublished manuscript). An asymmetric feather tip will give rise to unequal drag across the feather, while a symmetrical feather-tip will produce even drag across the tip (Møller *et al.* 1995b; A. P. Møller and A. Hedenström, unpublished manuscript). These comparative analyses suggest that the narrowing of the tail feathers of the males in species with exaggerated tails (a narrow tail feather is a tail streamer) acts as a general cost-reduction mechanism independent of foraging mode and tail shape.

Such means of cost reduction are commonplace in birds and other organisms (reviews in Hill 1994; Møller 1996) and suggest a combined role of natural and sexual selection in shaping the morphology of secondary sexual characters. We suggest that the Norberg mechanism is a secondary adaptation, evolved in response to mounting costs of ornamentation. If that is the case, the chain of evolutionary events is as follows. Sexual selection gave rise to exaggeration of the male trait, and the costs of this exaggeration caused by sexual selection were subsequently reduced by morphological adaptations that, in turn, allowed further exaggeration, and might have given rise to mechanisms enhancing aerodynamic efficiency such as the Norberg mechanism.

5. CONCLUSIONS

We have reviewed our detailed studies of natural and sexual selection in the barn swallow and found many independent classes of evidence for current sexual selection resulting from both natural and manipulated tail length of males. Empirical evidence also clearly demonstrates natural selection costs of tail elongation, but natural selection benefits from tail shortening, suggesting that tail length is displaced from the optimum under natural selection. These results consistently support sexual selection theory, but conflict with those predicted exclusively from an advantage due to natural selection, according to which any manipulation should result in a deterioration. Finally, aerodynamics cannot easily explain the evolution either of age and sex differences in tail length, or of geographical variation in sexual size dimorphism in the direction predicted by natural selection due to the Norberg effect. Sexual selection, by contrast, readily explains these observations. We do not claim that natural selection has not affected the evolution and the maintenance of secondary sexual characters in barn swallows, nor those of any other species, but based on empirical evidence we insist that sexual selection has profound effects on tail length in the barn swallow. The magnitude of the Norberg effect and its fitness consequences, if any, by contrast need observational and experimental confirmation.

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