COMMENTS

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SEXY STREAMERS? THE ROLE OF NATURAL AND SEXUAL SELECTION IN THE EVOLUTION OF HIRUNDINE TAIL STREAMERS

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Matyjasiak et al. (2000) reported recently on experiments designed to mimic the early stages of tail streamer evolution in barn swallows (*Hirundo rustica*) by adding small streamers onto a closely related species that lacks them, the sand martin (*Riparia riparia*). This work was interpreted as providing evidence that there is a cost associated with the initial evolutionary stage of a tail streamer and that higher-quality individuals are better able to withstand this cost than lower-quality individuals. The authors suggest that these results give support to the hypothesis that tail streamers initially evolved as a handicap (Zahavi 1975), rather than as a result of Fisherian selection (Fisher 1958), to advertise male quality. We would like to raise a number of issues, which may offer an alternative interpretation.

SEXUAL VERSUS NATURAL SELECTION PRESSURES IN TAIL STREAMER EVOLUTION

There is currently much debate as to the functional significance of elongated tail streamers in the barn swallow (e.g., Norberg 1994; Hedenström 1995; Evans and Thomas 1997; Evans 1998, 1999; Hedenström and Møller 1999; Buchanan and Evans 2000), but Matyjasiak et al. (2000) failed to mention this contentious issue. For example, Norberg (1994) proposed a mechanism by which streamers may aid aerodynamic performance by allowing birds to perform tighter turns, thus improving maneuverability and facilitating more efficient aerial hawking of large insects. Consequently, Norberg (1994) suggested that tail streamers could have evolved purely through natural selection; any initial elongation providing improvement in foraging success would lead to further elongation. Indeed, in support of this argument, a series of experiments have confirmed that the majority of the barn swallow's streamers can be attributed to natural selection, but have been extended past their aerodynamic optimum, presumably through sexual selection (Evans 1998; Buchanan and Evans 2000). This inevitably has implications for any interpretation of tail streamer evolution that assumes a purely sexual signaling function.

INITIAL SELECTION PRESSURE FOR TAIL STREAMERS?

Matyjasiak et al. (2000) observed that sand martins with elongated outer tail feathers caught smaller and less-profitable insect prey and concluded that the initial ornament imposed a considerable cost in terms of decreased flight performance. This is an interesting finding, but one we believe to be consistent with other explanations for tail streamer evolution. We have been investigating the direct aerodynamic consequences of initial streamer evolution by examining the effects of small tail elongations on two species of streamerless hirundines (Park et al. 2000; Rowe et al. 2001), one of which is the sand martin as in Matyjasiak's study. Sand martins with longer tail elongations (up to 20 mm) escaped faster from a flight maze than did individuals with shorter elongations (Rowe et al. 2001). In a different study (Park et al. 2000), we manipulated the tail lengths of house martins and measured changes in their free-flight performance. Three flight variables related to maneuverability improved with a small increase in the length of the outer tail feathers. In contrast, for mean velocity and mean acceleration the outer tail feathers appear to be at their optimum length and deviations from this caused a reduction in flight performance. Consequently, we suggest that the initial selection pressure for streamers in short-tailed ancestors of barn swallows was via natural selection for increased manoeuverability, but at the expense of flight variables associated with level flight (Park et al. 2000; Rowe et al. 2001).

That Matyjasiak et al. (2000) should have found a cost in terms of foraging ability is consistent with these results. Hirundines have presumably evolved from an ancestral streamerless state (Møller 1994). Swallows are generally considered to be the most maneuverable of the European hirundines, catching large, fast-moving prey (Turner and Rose 1989), whereas streamerless species appear to fly at higher flight velocities (unpubl. data) and catch smaller insects (Turner and Rose 1989). As such, improved maneuverability may not benefit the foraging success of present-day streamerless species, which have evolved to fly relatively fast and straight.

DIFFERENTIAL COSTS BETWEEN HIGH- AND LOW-QUALITY INDIVIDUALS?

Under the handicap principle, a signal of a given size must be more costly for a poor-quality individual than for a high-quality individual (Zahavi 1975). Matyjasiak et al. (2000) found that the foraging ability of female sand martins with originally longer outer tail feathers decreased by less than females with originally short outer tail feathers. They argue that this is evidence of the tail streamer acting as a handicap, which differs in its effect according to the individuals' quality. However, Matyjasiak et al. (2000) recognize that the addition of a small streamer on individuals with naturally longer outer tail feathers incurs a proportionally smaller increase in drag in comparison to those with short outer tail feathers, although they discount the importance of these effects. We would argue that such relative differences may have important implications for the interpretation of the results. Moreover, morphological variables covary. Our own data show that outer tail feather length correlates with wing length ($r^2 = 0.52$, $P < 0.05$, $n = 16$) and with central tail feather length ($r^2 = 0.61$, $P < 0.05$, $n = 16$; K. J. Park, unpubl. data). Short-tailed females may, therefore, experience a disproportionate cost in comparison to long-tailed females due to the covariance in morphological traits.

The results presented by Matyjasiak et al. (2000) are interesting and address the fascinating question of how selection pressures may initiate evolutionary changes in morphology. However, the interpretation that this provides evidence for a sexually selected pressure for initial tail streamer evolution through the handicap principle is not convincing. We offer an alternative explanation that the initial selection pressure for streamers in short-tailed ancestors of barn swallows was via natural selection for increased maneuverability, but that in present-day sand martins and house martins this potential benefit is outweighed by the detrimental effect of streamers on other flight variables that, in this case, may be more important to their feeding ecology.

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HYPOTHETICAL MECHANISMS OF THE INITIAL EVOLUTION OF SEXUALLY DIMORPHIC TAIL STREAMERS IN *HIRUNDINIDAE*

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The functional significance of long tail streamers (ornamental outermost tail feathers) in male barn swallows *Hirundo rustica* has been the subject of many recent debates (Norberg 1994; Hedenström 1995; Evans and Thomas 1997; Møller et al. 1997; Barbosa and Møller 1999; Evans 1999; Hedenström and Møller 1999). The initial selection pressures for tail streamers are unknown. Our study of this problem (Matyjasiak et al. 2000) triggered a comment from Park et al. (2001) to which this note responds.

We imitated the initial development of streamers typical of male barn swallows by lengthening the outermost tail feathers in sand martins (*Riparia riparia*), a closely related streamer-less species that resembles hypothetical ancestral ''barn swallows'' with respect to tail morphology (Matyjasiak et al. 1999, 2000). We found that birds with initial streamers captured smaller insects than controls. Our results suggested that these initial streamers imposed a cost in terms of handicapped foraging, and that naturally long-tailed sand martins were better able to cope with this initial ''ornament'' than naturally short-tailed ones. Assuming that some females display initial preference for long streamers and that initial streamers impose costs upon individuals, we suggested two mechanisms that may have been involved in the initial evolution of sexually dimorphic tail streamers. First, a handicap mechanism (Zahavi 1975) might have been important from the very beginning. Poor individuals might have incurred a larger decrease in foraging performance associated with tail elongation, and therefore developed shorter streamers. As a result, shorter streamers reliably indicated poorer individuals. Second, a correlation between physical condition and streamer length might have developed as a result of initially condition-independent decline in foraging performance. It might have happened due to higher aerodynamic costs of elongated streamers to initially short-tailed than to initially long-tailed individuals, combined with condition dependent ability to deal with impaired foraging performance (see Discussion in Matyjasiak et al. 2000). We agree with Park et al. (2001) that an artificial streamer of the same length may induce proportionally greater increase in drag when added to a short tail than when added to a long tail. Although the authors unjustifiably stated that we have ''discounted the importance'' of such aerodynamic costs (see above and Matyjasiak et al. 2000), they supplemented our reasoning by pointing out that short-tailed birds may experience a disproportionate cost compared to long-tailed ones due to the covariance in morphological traits (e.g., shorter tails correlate with shorter wings). We are aware of the importance of this effect, and are performing another set of experiments designed to control for it.

Park et al. (2001) have proposed an alternative explanation for the origin of tail streamers, which assumes a natural selection advantage in terms of foraging to individuals with initial streamers. The authors report on two tail-manipulation experiments in which small streamers were added onto streamer-less hirundines (sand martins and house martins *Delichon urbica*), and direct aerodynamic consequences of wearing those streamers were measured. The studies in both species showed that even initial streamers could improve flight maneuverability, but at the expense of those flight variables (velocity and acceleration) that were associated with fast level flight (Park et al., 2001; Rowe et al., in press). Park et al. (2001) conclude that the initial selection pressure for streamers in ancestral streamer-less ''barn swallows'' was via natural selection for enhanced maneuverability to increase foraging success, and not via sexual selection for advertising quality. A study that shows experimentally an increase in prey size with elongation of streamers from ancestral short-tailed state toward the predicted optimum for maneuverability would strongly support this mechanism. No such experiments have been published, but Møller et al.'s (1995) data do not contradict such a possibility (Rowe et al., in press). However, our data (Matyjasiak et al., unpubl. ms.) suggest that the very initial streamer elongation in the barn swallow may have little or no functional explanation in terms of increased flight maneuverability. We have applied a flight maize task (adapted from Møller 1991) to investigate the impact of streamer removing or streamer lengthening upon maneuvering flight in juvenile barn swallows during autumn migration. Juvenile barn swallows have streamers that do not exceed 10 mm in length and do not project outside the maximum tail span in a spread tail (Møller 1994). Short tail streamers in juvenile barn swallows were suggested to be close to the optimum under natural selection (Cuervo et al. 1996), whereas both natural and sexual selection (Evans 1988; Buchanan and Evans 2000) shape adult tail streamers. We found that the removing of streamers in juvenile barn swallows, so that they resembled ancestral streamer-less ''barn swallows,'' did not affect maneuverability, whilst lengthening streamers, imitating later evolutionary stages of streamer elongation, enhanced maneuverability. Consequently, we suggest that sexual selection for genetic quality rather that selection for maneuverability might have shaped the very initial elongation of the sexually dimorphic tail streamer in the barn swallow (Matyjasiak et al., unpubl. ms.).

The results and interpretations presented by Park et al. (2001) are important because they suggest that the early streamer elongation could be due to selection through mate choice for better parental performance. Such an initial sexual selection might have given direct phenotypic benefits to both the choosing and the chosen sex. We do not disregard this mechanism. However, we lean toward a more likely (in the light of currently available data) mechanism that streamers in streamer-less ancestors of modern barn swallows were initially selected via sexual selection for advertising quality.

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