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

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In this comment we review some experiments, which address the initial selection pressures promoting the development of tail streamers in some hirundine species. The results of recent experiments have been interpreted as providing evidence for the hypothesis that tail streamers evolved as a handicap, through sexual selection. We offer an alternative explanation with evidence from our studies which suggest that tail streamers may have evolved initially through natural selection for increased manoeuvrability, and would not therefore originally act as a handicap.

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 which lacks them, the sand martin (*Riparia riparia*). This work was interpreted as providing evidence that 1) there is a cost associated with the initial evolutionary stage of a tail streamer, and 2) 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.

1. 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; Evans 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 and thus improving maneuvrability, 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 streamer of the barn swallow can be attributed to natural selection but has been extended past its 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 signalling function.

2. Initial selection pressure for tail streamers?

The authors 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 streamer-less hirundines (Park et al. in press; Rowe et al. in press), one of which is the sand martin as in Matyjasiak's study. Sand martins with longer tail elongations (up to 20mm) escaped faster from a flight maze than did individuals with shorter elongations (Rowe et al. in press). In a different study (Park et al. in press) we manipulated the tail lengths of house martins and measured changes in their free-flight performance. Three flight variables related to manoeuvrability 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 the short-tailed ancestor of modern barn swallows was via natural selection for increased manoeuvrability but at the expense of flight variables associated with level flight (Park et al. in press; Rowe et al. in press).

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 streamer-less state (Møller 1994). Swallows are generally considered to be the most manoeuvrable of the European hirundines, catching large fast moving prey (Turner and Rose 1989), whilst streamer-less species appear to fly at higher flight velocities (unpubl. data), and catch smaller insects (Turner and Rose 1989). As such, improved manoeuvrability may not benefit the foraging success of current day streamer-less species, which have evolved to fly relatively fast and straight.

3. 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, the authors recognise 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 co-vary. Our own data show that outer tail feather length correlates with wing length ($r^2 = 0.52$, $P < 0.05$, $n = 16$), and also with central tail feather length ($r^2 = 0.61$, $P < 0.05$, $n = 16$) (K.J. Park unpublished 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 the short-tailed ancestor of modern barn swallows was via natural selection for increased manoeuvrability, 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 which, in this case, may be more important to their feeding ecology.

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