

Report

Uninformative Exaggeration of Male Sexual Ornaments in Barn Swallows

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Summary

Models of sexual selection suggest that mate-choice preferences are favored because differences between males in their degree of ornamental exaggeration convey useful information about the direct or indirect benefits they have to offer [1–5]. Such arguments assume that variation in male ornament size can be attributed to variation in the degree of sexually selected exaggeration. We provide the first test of this assumption by conducting tail-length experiments in male barn swallows. Over the last twenty years, a large amount of work has shown that female barn swallows are influenced by male tail length when choosing a mate [6–12]. Recent experiments have shown that a combination of natural and sexual selection results in the elongated tail streamer—a tail that is on average across the population about 12 mm (~10%) longer than the aerodynamic optimum [13, 14]. We show that the aerodynamically optimal tail length varies significantly between males, whereas the extent of streamer elongation beyond the optimum does not. Similarly, the aerodynamically optimal tail length significantly predicts observed tail length and conveys information about flight performance, whereas the extent of sexually selected exaggeration of streamer length does not. Therefore, contrary to handicap models of sexual selection, the sexually selected exaggeration of this trait provides females with little information about any aspect of mate quality.

Results and Discussion

Traits that have become elaborated by sexual selection usually also serve some other, naturally selected function. For instance, the elongated tails of many male birds

provide some of the best-known examples of sexual selection [15], but also have an important aerodynamic role, particularly in slow flight and during maneuvers [16]. For a trait that is the product of both natural and sexual selection, it will always be unclear whether individual variation in ornament size reflects variation in the degree of sexually selected exaggeration, or simply variation in the size of the underlying naturally selected optimum trait value.

Over the last 20 years, studies on the barn swallow have shown that females prefer to mate with males with experimentally elongated tails [6, 8, 9, 17] and that these males also suffer a viability cost in future years [7] but that females provision the broods of long-tailed males more frequently [18, 19]. Males with naturally long tails arrive from wintering grounds earlier [20], have higher viability [10], have chicks with fewer parasites [21], and experience lower rates of paternity loss [22]. However, recent studies of the elongated tail streamers of male barn swallows have shown that a substantial part of the streamer has an aerodynamic function [13, 14, 23], although the trait has been elongated beyond the aerodynamically optimal length by sexual selection. On average, the naturally selected optimal length is approximately 95 mm, and the extent of sexually selected elongation beyond this is about 12 mm. The daily energy expenditure of swallows has also been shown to vary in a curvilinear fashion with a peak in energy expenditure at 119 mm; this was interpreted as being due to differences in the way in which the tail was used by males with different tail lengths. If this is the case, then both foraging ability and flight performance would be expected to vary with tail length in a nonlinear manner [24].

To partition observed variation in swallow streamer length into naturally and sexually selected components, we determined the aerodynamically optimal length for each of a sample of male barn swallows by conducting serial streamer-length manipulations on individual birds. In doing so, we assume that the aerodynamically optimal tail length will be that which maximizes maneuverability or the mean size of captured prey; this will be true if natural selection is acting on streamer length with respect to these tasks and if there are no constraints preventing a response to selection. That aerial foraging ability and maneuverability should be important currencies for an obligate aerial insectivore does not seem an unreasonable assumption. Swallows fly with their tail streamers in the breeding and wintering grounds as well as during migration, so the cumulative consequences of even small deviations from optimum are likely to be large over a year.

The curves that related maneuverability (tested with a flight maze) and prey size (estimated from fecal samples) to manipulated streamer length were estimated for individual birds. The streamer lengths that maximized maneuverability and prey size were calculated from these curves by differentiation, producing two

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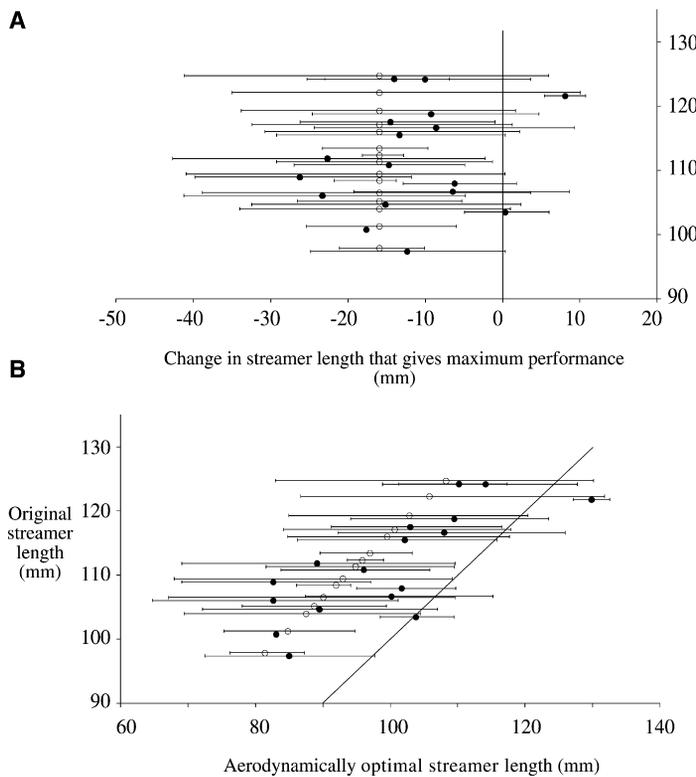


Figure 1. The Between-Male Variation in the Naturally and Sexually Selected Components of Streamer Length as Defined by Maneuverability and Prey Captured

(A) The amount by which streamer length has to be changed to give maximum performance varies slightly for each individual male swallow but does not vary systematically with original streamer length (maneuverability, $F_{1,15} = 0.86$, $p = 0.37$; diet, $F_{1,13} = 0.01$, $P = 0.92$).

(B) Aerodynamically optimal tail length varies considerably among males, and does vary significantly with original streamer length (maneuverability, $F_{1,15} = 22.48$, $p < 0.001$; diet, $F_{1,13} = 75 \times 10^7$, $p < 0.001$); the line represents the point at which original streamer length = aerodynamically optimal streamer length. Solid symbols show results for maximum maneuverability as measured by time to negotiate the flight maze, and open symbols show results for mean mass of individual prey items recorded in feces. These two figures are estimated separately for each bird; a small amount of vertical jitter has been added to display values clearly. The figures show the estimated position of the mean (\pm standard deviation [SD]) for each bird (produced from 999 bootstrapped estimates of the model coefficients). The apparent uniformity of the estimates for the diet analyses is due to the much lower amount of variance explained by the individual identity terms in the diet model than in the maneuverability model when the data are plotted on the same scale then the scatter in the diet data is diminished.

estimates of the aerodynamically optimal tail length for each individual. We predicted that if the observed variation in streamer length was due to variation in the extent of sexually selected exaggeration of the ornament, then the amount by which the tail streamer needed to be reduced to reach the aerodynamically optimal tail length (the value of manipulation that solves equation 3) should increase with observed tail length. If, however, the observed variation in streamer length was due to variation in the naturally selected component of tail length, then the aerodynamically optimal tail length should vary with observed tail length. Figure 1 shows that there was no relationship between the degree of exaggeration beyond the estimate of the aerodynamic optimum and the observed tail length (Figure 1A), whereas aerodynamically optimal tail lengths vary in parallel with observed tail length (Figure 1B). These results are consistent with the hypothesis that observed variation in tail length is due to variation in the aerodynamically optimal tail length and is not consistent with the hypothesis that observed variation in tail length is principally due to variation in the degree of sexually selected exaggeration.

Additional analyses reveal that whereas the aerodynamically optimal tail length shows significant between-individual variability ($F_{1,13} = 4.18$, $p = 0.006$), the extent of sexually selected exaggeration beyond the optimum does not ($F_{1,13} = 0.83$, $p = 0.38$). It is known that female swallows use male streamer length as a cue for mate choice [6, 8], which suggests that the length of the tail streamer contains useful information. Our analyses suggest that variation in the length of the

naturally selected component of the tail streamer is a good predictor of observed streamer length, explaining a significant 60% or more of the variance in observed streamer length (Figure 2A). However, variation in the sexually selected component only explains a nonsignificant 5% of variation in the length of the total streamer (Figure 2B). The slope of the regression that relates the estimated length of the naturally selected part of the streamer to observed streamer length does not differ significantly from unity (maneuverability, $t_{16} = 1.09$, $p = 0.30$, prey capture, $t_{15} = 0.01$, $p > 0.90$), so the most parsimonious model for both measures of flight performance is as follows: observed streamer length = naturally selected streamer length + constant.

These analyses are consistent with the hypothesis that it is variation in the underlying naturally selected trait that produces the differences in tail length between individual male swallows. It is also worth reiterating that although there is exaggeration in the length of the tail streamer beyond the aerodynamic optimum, this does not vary significantly between individual males. This means that if female swallows use tail length as a cue to discriminate between males, they are likely to be doing so on the basis of variation in the underlying naturally selected trait and not on the extent of ornamentation beyond this optimum.

Females should choose males by using traits that convey useful information about male quality. The conventional view is that the extent of exaggeration of the ornament should be related to male quality such that males of higher quality should produce larger

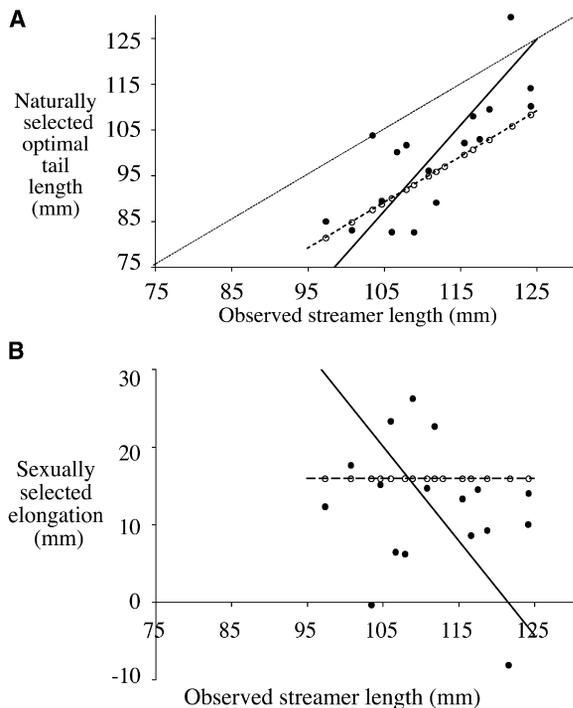


Figure 2. The Relationships between the Naturally and Sexually Selected Components of Streamer Length and Observed Streamer Length

(A) The size of the naturally selected part of the tail streamer covaries closely with observed streamer length, explaining 60%–99% of the variation in observed streamer length (maneuverability, $F_{1,15} = 22.48$, $p < 0.001$; diet, $F_{1,13} = 7.6 \times 10^8$, $p < 0.001$). The least-squared regression lines are drawn through the points; neither of the slopes of the lines is significantly different from unity. The line of equality is shown for comparison (dotted).

(B) The extent of sexually selected exaggeration of the streamer is not significantly related to original streamer length, explaining less than 5% of the variation in observed streamer length (maneuverability, $F_{1,15} = 0.86$, $p = 0.37$; diet, $F_{1,13} = 0.001$, $p = 0.98$). Points derived from the analysis of maneuverability data are filled and have a solid line; those from diet analysis open with a dashed line. In both panels, each bird is represented by a single symbol.

ornaments. Our finding that there is no significant variation among individuals in the extent of exaggeration argues against this possibility in the case of swallow streamer length. However, if there is meaningful variation in the underlying naturally selected trait, then this might nevertheless reflect male quality. We have used the individual functions relating flight performance to manipulation in order to examine whether the predicted flight performance at optimal streamer length (maximal performance) is related to either the naturally selected component of streamer length or the extent of sexually selected exaggeration (Figure 3). Taken alone, neither of these factors explains significant variation in maximal maneuverability (sexually selected component, $r = 0.03$, $n = 17$, $p = 0.89$; naturally selected component, $r = -0.30$, $n = 17$, $p = 0.23$). However, if the other aspect of tail morphology measured on birds during this experiment (length of central tail feather) is taken into account, then variation in the length of the naturally selected component of the streamer significantly predicts maximum maneuverability ($F_{1,12} = 4.73$, $p < 0.005$). It is not unreasonable that the length of the central tail feather might

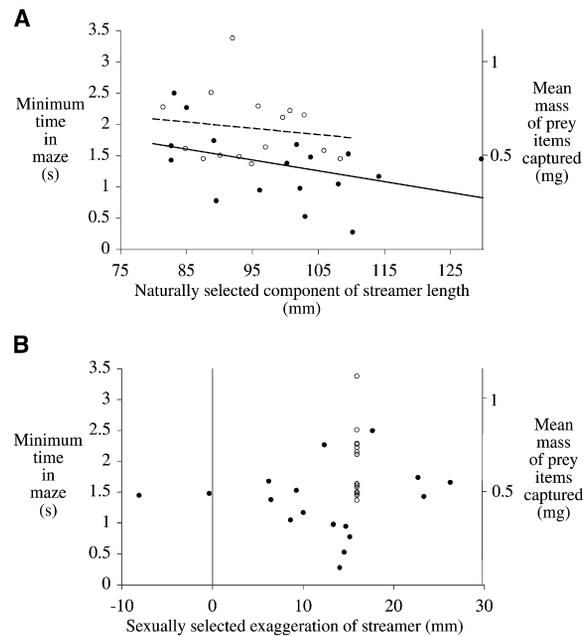


Figure 3. The Relationships between the Naturally and Sexually Selected Components of Streamer Length and Maximum Performance

Females use a trait to select between males because it conveys useful information about male quality. If females are interested in a given aspect of male performance, then we would expect that the trait would covary with that measure of performance.

(A) Variation in the length of the naturally selected part of the streamer predicts both maneuverability (when another aspect of tail morphology is also taken into account) and mean mass of prey items captured.

(B) The extent of sexually selected exaggeration predicts neither maneuverability (either alone or in combination with any other aspect of morphology) nor mean mass of prey items captured.

In both panels, each bird is represented by a single symbol; filled symbols and solid lines relate to maneuverability, and open symbols and dashed lines relate to mean mass of individual prey items.

explain some variation in maneuverability because it sets the size of the tail surface that generates lift through delta wing aerodynamics [25]. In contrast, no aspect of morphology measured on birds during this experiment results in a significant relation emerging between variation in the extent of sexually selected exaggeration and maximum maneuverability when variation in morphological traits was included in an analytical model either as a factor or as a combination of factors (Figure 3). These results suggest that males with longer naturally selected components of streamer length are more maneuverable than males with shorter naturally selected components of streamer length. Thus, females could gain useful information about flight performance of males by assessing streamer length. Flight performance may be an important trait for a female to assess because it will influence the direct benefits that she gains through the male's foraging ability, but it may also be heritable, such that the offspring of males with good flight performance may inherit this trait and so perform well themselves, both enhancing their survivorship and their future reproductive success [1].

It was Darwin who first explained the elaborate male ornamentation of many dimorphic species as an outcome of sexual selection [26]. Over the last 20 years, a great many studies have verified his suggestion that

females will mate preferentially with those males whose ornaments are the most extreme within the population [15]. Handicap models suggest that such preferences are favored because differences between males in their degree of ornamental exaggeration convey useful information about the direct or indirect benefits they have to offer [1–5]. Existing models of sexual selection typically assume that attractive traits serve a purely ornamental function—that is, the naturally selected optimal trait value is zero for all individuals, which means that variation in male ornament size can be attributed to variation in the degree of sexually selected exaggeration [1–5]. Consequently, differential expression of the trait by individuals of low and of high quality must reflect differences in the extent of deviation from the optimum value of zero. Female mate preferences for extreme ornaments are assumed to be favored because the degree of deviation is informative—for instance, if high-quality individuals experience lower costs of exaggeration, they may be expected to exhibit more exaggerated trait values that deviate further from their naturally selected optima. We have shown, however, that it is variation in the underlying naturally selected optimum itself, rather than in the extent of deviation from it, that accounts for the observed variation in size of the tail streamers of swallows. This finding suggests that sexually selected exaggeration has added little to the information content of the signal—the relatively invariant sexually selected component of the streamer may do little more than facilitate discrimination between the sexes (it is worth noting that the mean difference between male streamer length and female streamer length in European barn swallows is 12 mm [27], similar to the value reported here for sexually selected exaggeration). The fact that the sexually selected component of streamer length varies little between males also argues against the possibility of its being used as an amplifier of variation in the naturally selected part (otherwise, you would expect to see the two elements of streamer length covary) [28].

Although Fisher [29] suggested that female preferences might originate as a response to pre-existing cues of quality, this possibility has received little subsequent attention. We are aware of only one study, on stalk-eyed flies, that provides evidence that a sexually selected ornament has evolved through exaggeration of a trait that, even in its original state, was an indicator of male quality or condition [30]. Moreover, even in this case, the data indicate that the heightened condition dependence of the ornament is associated specifically with its elaboration [30]. Our results, by contrast, show that costly exaggeration of a display trait need not always lead to increased information content (as is widely assumed [30–32]), and suggest that naturally selected cues of quality may play a more important role in sexual selection than is currently envisaged.

Experimental Procedures

Experimental Design

Thirty-two male swallows were captured in mist nets at breeding sites around Stirling University between April and September, 2003, and each bird was ringed and marked on the breast with a unique combination of colored dyes, which allowed individual identification while in flight. At capture, various morphological measurements were taken from each bird—right and left streamer

lengths (mm), length of central tail feather (mm), tarsus length (mm) (all measured with digital callipers, to nearest 0.1 mm), body mass (g) (with Pesola spring balance to nearest 0.1 g), and maximum chord wing length (mm) (with stopped rule to nearest mm). Birds were manipulated in a random sequence so as to remove any confounding effect of date. This meant that after the first occasion, streamers might have to be elongated or shortened with respect to their current length (depending on the previous manipulation). Reduction manipulations were conducted following a technique used previously [13, 14, 33] in which the required amount is trimmed from the end of the tail streamer. If the new manipulation was longer than the previous manipulation, then an alternative technique was used: The streamer was cut at about 15 mm from the base, and a new streamer (obtained from males caught on other farms early in the field season) was attached to the stump. The new streamer was cut so that the shoulder of the broad basal section of the feather lay in the same place as the original feather. The new feather was butted against the stump and held in place by insertion of a 0.35-mm-diameter fishing line into the hollow of the central rachis of both the stump and the new feather, which was secured with Loctite superglue. This elongation technique proved very successful, with no breakages recorded during the season. The manipulation type was included in the starting analysis as a binary variable but failed to significantly explain variance.

We investigated the aerodynamically optimal length of streamers in individual swallows by performing random sequential manipulations on the same bird [13, 14, 23]. At each capture, birds were assigned randomly to a treatment group in which streamers were shortened by 0, 3, 6, 10, 15, or 20 mm. We only conducted reduction manipulations because we have shown previously that tail streamers are longer than the aerodynamically optimal length [23] and because there are logical reasons to believe that only reduction manipulations could reveal the position of the optimum in this case [34].

Assessment of Maneuverability

Birds were caught and assessed for maneuverability 4–10 days after manipulation; they were then released, and attempts were made over the following 2 days to capture the birds for the next manipulation.

Maneuverability is usually defined as the tightest turn that can be made by a flying animal. The usual way to assess maneuverability is to use a flight maze; these were originally used in bats [35, 36] but more recently have also been used with birds [14, 23, 35–37]. It should be noted here that we have chosen to try to assess a biologically and ecologically relevant measure of flight performance rather than a more abstract aspect of aerodynamics such as minimum energy costs. Immediately after manipulation, birds were released through a flight maze designed for use with swallows. The maze consisted of an 8-m-long flight cage with about 400 vertical strings as obstacles. String spacing decreased steadily along the length of the maze, so that the birds were forced into making increasingly tighter maneuvers. As is usual when a maze is used, the number of strings hit during the flight was recorded, and the time taken to fly through the maze was measured by a video camera positioned at the open end of the maze and large angled mirrors used to view the entrance to and the exit from the stringed section of the maze. The entire flight through the maze was filmed and then examined frame-by-frame as described in [14]; we were therefore able to measure the time taken to fly through the maze with an accuracy of 0.04 s. This methodology has previously been used to quantify optimal streamer lengths in swallows and sand martins (*Riparia riparia*) [14]. The criterion for inclusion in the final dataset was that the bird had to be flown through the maze with at least four different tail lengths. This criterion meant that the final analyses were performed on a sample of 17 males, providing among them data on 86 flights through the maze. The number of birds in each treatment group was as follows: 0 tail-length manipulation, 14 birds; –3, 12 birds; –6, 14 birds; –10, 15 birds; –15, 14 birds; and –20, 17 birds.

Assessment of Prey Caught

At each capture event, any feces produced by the birds (in the bags in which they were kept between capture and manipulation—a maximum of 20 min) were collected and stored in 70% alcohol. Therefore,

the feces produced by a bird would have contained prey captured while the bird was flying with the tail length it had at capture (which it would have had for a period of 4–10 days). Subsequently, prey remains in feces were identified to order by the use of keys [38–40], and intact wing lengths were measured under a binocular microscope to the nearest 0.1 mm. Wing lengths were converted to estimated dry mass through order-specific algorithms [41]. Estimates were thus made of the dry mass of individual prey items caught and consumed by birds with different tail-length manipulations. The criterion for inclusion in the final dataset was that the bird had prey remains identified from feces collected when it had at least four different tail lengths. This meant that the final analyses were performed on a sample of 15 males.

Data Analysis

The time taken to fly through the maze and the mean dry mass of prey were used as dependent variables in a mixed-model ANOVA analyzed with ReML on R version 2.0.1. Individual identity was included as a random effect, with manipulation, manipulation², date of manipulation, number of strings hit (for maneuverability analysis), and whether or not the rachis was glued basally as fixed effects. The individual-specific slopes and intercepts were obtained by including manipulation² and manipulation terms as slopes in the random model. These models were used to generate individual-specific curves of the form:

$$y = \text{individual-specific constant} + (a + a_i) \times \text{manipulation}^2 + (b + b_i) \times \text{manipulation} \quad (1)$$

where a_i and b_i are individual-specific adjustments to the coefficients for manipulation² and manipulation, respectively.

Because we were interested in the tail lengths that would give the minimum time spent in the maze (defined as maximum maneuverability [14]) and maximum prey mass (larger prey are more profitable [41]), we needed to determine the tail lengths at the minima and maxima of the maze-time and prey-size functions. Differentiation of the individual-specific equations (equation 1) can then be used to produce an estimate of the value of manipulation at the turning points of these equations, which occur when the first differential = 0:

$$dy/dx = 2(a + a_i) \text{manipulation} + (b + b_i). \quad (2)$$

Setting (2) to zero and rearranging gives:

$$\text{manipulation at turning point} = -(b + b_i)/2(a + a_i). \quad (3)$$

Equation 3 was solved for each bird with both maneuverability and diet data where available to provide estimates of the tail-length manipulations at the turning points of the individual-specific equations. Bootstrapping of the model coefficients (using the boot routine within R) was used to produce variance estimates around these values. These analyses can be conducted in two ways—through the use of either manipulation (the amount that was experimentally removed from the tail streamer) or current tail length as the independent variable in the analysis. These approaches gave estimates of the extent of sexually selected exaggeration and the aerodynamically optimal tail length, respectively, which were used as independent variables explaining variance in observed streamer length, minimum time taken to fly through the maze, and maximum mean prey size. For all these analyses, reduced-major-axis regression was used to generate the regression lines. This is due to the fact that there is error in the values on both the x and y axes [42]. However, given that least-squared approaches are more conservative, traditional least-squared regression has been used to generate the statistics associated with these lines.

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