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The function and evolution of the tail streamer in hirundines

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The morphology of a bird's tail may result from compromises between aerodynamic efficiency, phylogenetic constraints and selection for non-aerodynamic characteristics, such as mate attraction. A good example of a trait shaped by trade-offs between aerodynamic efficiency and reproductive benefits mediated through female preference is the tail streamer of the barn swallow. Here we use a standardized task to measure the impact of manipulated tail streamer lengths on maneuvering flight in the barn swallow and in the sand martin, a closely related species that lacks a streamer. Our results show that the tail streamer of the barn swallow has a role in maneuvering flight. However, the outer tail feather is approximately 12 mm (9–20%) longer than the aerodynamic optimum for maneuvering flight. Furthermore, we show that the addition of artificial tail streamers to the sand martin, enhances maneuverability even at small streamer lengths, thereby implying that tail streamers may have evolved via natural selection for increased flight performance. Our results therefore suggest that initial tail streamer elongation in the barn swallow has a functional explanation in terms of increased aerodynamic performance. However, female choice has become associated with this trait, promoting the development of a costly handicap. *Key words:* flight performance, *Hirundo rustica,* maneuverability, natural selection, Norberg mechanism, *Riparia riparia,* sexual selection. *[Behav Ecol 12:157–163 (2001)]*

Darwin (1871) was the first to attribute many exaggerated ornaments, such as the elongated tails of birds, to sexual selection. Many studies have since demonstrated that such ornaments have important implications for mate choice, with females preferring males with more exaggerated traits (reviewed in Andersson, 1994). Although the exact mechanism is much in dispute (Andersson and Iwasa, 1996), such traits are thought to become established in a population through an association with female choice, either via a runaway process (Fisher, 1930), or through selection for high phenotypic or genetic quality (Hamilton and Zuk, 1982, Zahavi, 1975, 1977).

One of the classic examples of a sexually selected ornament is the elongated outer tail streamer of the barn swallow (reviewed in Møller, 1994). Male swallows possess long streamers and an average tail length of 108 mm, while female barn swallows have considerably shorter streamers and an average tail length of 90 mm (Møller, 1994). Females have been shown to exhibit a mate preference for long tailed males (Møller, 1988). In addition, extra pair copulations, paternity, and therefore reproductive success also vary with male tail length (Møller and Tegelström, 1997; Saino et al., 1997). The tail streamer is thought to be condition-dependent (Møller, 1991a), while cross fostering experiments suggested that both parasite resistance (Møller, 1990a) and male tail length have a genetic basis (Møller et al., 1998). Such evidence supports the theory that the streamer acts as a signal of individual genetic quality, which could be used by females during mate choice.

Only recently have the aerodynamic properties of the tail streamer been considered (Evans, 1998; Evans and Thomas, 1997; Norberg, 1994; Thomas, 1993a). Application of delta wing theory has concluded that only the area in front of the point of maximum continuous span is aerodynamically important, as it generates lift. According to this hypothesis, the streamers should only generate drag (Thomas, 1993a). However, the flexible nature of the streamer may allow the leading edge to be deflected forming a vortex flap allowing lift to be generated at high angles of attack (Norberg, 1994). The presence of tail streamers would therefore improve maneuverability in slow turning flight.

Traits such as elongated streamer tails, could have evolved under purely natural selection, purely sexual selection or a combination of the two selection pressures. It is possible to distinguish between these three hypotheses by experimentally reducing streamer length and investigating the effect of such manipulations on flight performance. Sexual selection predicts a positive relationship between maneuverability and streamer reduction whereas natural selection predicts a negative relationship. The combination of both natural and sexual selection is the only scenario that predicts a curvilinear relationship as tail length is progressively reduced (Evans and Thomas, 1997). Recent studies have shown part of the tail streamer of the barn swallow to have an aerodynamic function (Buchanan and Evans, 2000; Evans, 1998). In a recent study using stereo video filming to assess flight performance it has been shown that the last 10–15 mm of the tail streamer reduces aerodynamic performance and therefore can be viewed as costly and thereby be attributed to sexual selection, whereas the remainder of the tail streamer was found to enhance flight performance and can therefore be attributed to natural selection (Buchanan and Evans, 2000). It follows therefore that the tail streamer of the barn swallow is most probably the result of a combination of natural and sexual selection pressures. However, the original pressures selecting for the evolution of the tail streamer remains to be verified. If the initial driving force for the streamer elongation was natural selection, it would be necessary for relatively short streamers to be beneficial for flight, to instigate streamer development. However, if the original selection pressure for the tail streamer was sexual selection, females should show a mate preference for males with the slightest tail elongation. The tail streamer could have evolved initially through natural selection selecting for maneuverability and then been subject to sexual selection pressures elongating the streamer beyond its aerodynamic optimum. Alternatively, it may have been instigated through sexual selection with the Norberg effect acting as a cost-reducing

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mechanism. Therefore, it seems equally likely that the tail streamer could have evolved initially through either natural or sexual selection. The best way to examine the initial mechanism promoting streamer elongation in the barn swallow is to examine the effects of small streamers on the flight performance of a closely related streamer-less hirundine species. The sand martin (*Riparia riparia*) is similar to the barn swallow in foraging ecology and tail morphology (Turner and Rose, 1989) but lacks tail streamers.

The aims of this study were first to test experimentally how the streamer contributes to maneuverability and consequently to examine the relative roles of natural and sexual selection in determining tail shape in the barn swallow. Second, we sought to determine which mechanism initially promoted streamer development using experimental manipulation of a hirundine species without a tail streamer, the sand martin, to assess the effect of short streamer lengths on maneuvering flight performance.

In this study, a flight maze was used in order to assess maneuverability in a standardized manner. Such mazes have been used in previous studies of both bats (Aldridge, 1986; Aldridge and Rautenbach, 1987) and birds (Evans et al., 1994; Møller, 1991b). The time taken to fly through the maze and/or the number of contacts made while flying through the maze are taken as measures of maneuverability. The main advantage of the maze is that it is a standardized task and thus has advantages over assessing flight in the field. It also forces the bird to maneuver tightly (the distal spacing of the maze obstacles is half wingspan); this will force the birds to fly at close to their limits. The disadvantage of the maze is that it is unclear how maze performance relates to more ecological measures of performance such as foraging efficiency.

METHODS

Manipulations

Swallows

Barn swallows of both sexes were caught on farms in Stirlingshire using mist nets from May to August 1997. The birds were randomly assigned to one of seven treatment groups; six experimental and one control. The experimental groups had 2, 4, 8, 10, 15, or 20 mm of streamer removed from the end of their outer tail feathers. The control group were handled and measured in the same manner as the experimental groups but no feather was removed. The amount to be removed was measured from the end of the feather and the feather cut and trimmed to mimic the end of a natural feather. This may have resulted in some changes in the flexibility of the feather, but as the largest manipulation was only 20 mm, changes in the diameter of the central rachis at the end of the feather post-manipulation, were minimal. A number of body measurements were taken (wing length [mm], tail length [mm] before and after manipulation, head and bill length [mm] and mass [g]); and the birds were sexed according to a combination of presence/absence of brood patch and tail length.

Sand martins

Birds were caught at breeding colonies around Stirling, UK, and randomly assigned to one of eight treatment groups, seven experimental and one control. The experimental birds had sections of sand martin tail feather 2, 4, 6, 8, 10, 15, or 20 mm added to the end of the outer tail feathers using cyanoacrylic superglue. The added feather sections were trimmed into thin shapes modeled on the streamers of swallows. The control group were not elongated but received the same amount of handling. Measurements of wing length (mm), outer tail and mid tail lengths (mm), head and bill (mm) and mass (g) were taken and the birds were sexed according to size of brood patch (Svensson, 1975).

Flight maze

In order to assess maneuverability during flight, a standardized task was constructed which consisted of a flight maze (18 m × 4.5 m × 1.5 m) adapted from Evans et al. (1994). The frame of the flight maze was constructed from plastic drainpipe, reinforced with steel rods, which was covered in mesh and left open at one end. The birds were released from a box at the closed end and flew the length of the maze and out of the open end. The first 9 m of the maze, containing the release box, was free of obstacles and acted as an acceleration zone. From nine to eighteen meters there were successive rows of strings suspended from the roof of the maze. Both the distance between the strings within a row and the inter row interval decreased towards the exit. The strings at the end of the acceleration zone were spaced at 70 cm (approximately twice the wingspan of a barn swallow), while those at the end of the maze were spaced at 8.5 cm (approximately a quarter of a wingspan of a barn swallow). The advantage of a flight maze is that it presents a bird with a standardized task, which forces it to perform increasingly tight turns around obstacles. The stringed segment of the maze is a cluttered environment and a bird's performance in this section of the maze can be used to estimate maneuverability. It can be assumed that birds will attempt to escape after release. Hence they will try to minimize time spent in the maze. The time taken for an individual to fly out of the maze was taken as a measure of an individual's ability to fly efficiently through the cluttered maze environment. In addition to the time taken to fly through the stringed segment of the maze the number of strings an individual collided with was also recorded. The number of strings hit is included as a covariate as it seems intuitively reasonable that these two parameters should covary.

Flight analysis

The flight time through the maze was estimated from video images obtained with the use of angled mirrors placed in line with the first and last line of strings. A bird's image was reflected in the first mirror as it entered the stringed segment of the maze and in the second mirror as it left the maze. The time taken for a bird to fly through the stringed segment of the maze was taken as the number of frames on the video between the two images of the bird in the mirrors and therefore had an accuracy of 0.04 s. The number of strings hit by each bird was counted by observing any movement in the strings, by an independent observer, positioned at the open end of the maze who was blind to the manipulation. Birds were released through the maze immediately after manipulation.

Statistical analysis

The use of the flight maze results in two measures of maneuverability—time taken to fly through the stringed section and the number of strings hit. These two variables are likely to be inter-related. We have taken two approaches to the analysis of these data. First, we have used MANOVA models with flight time and number of strings hit as dependent variables and manipulation (both linear and quadratic terms) as the independent variables. Secondly, we used a general linear model ANOVA, using both flight time and number of strings hit as dependent variables. Three models were used:

- A simple analysis that included only manipulation as a categorical variable. This analysis demonstrates whether any manipulation groups were different from the overall mean.

- Using manipulation as a continuous variable (both linear and quadratic terms) which demonstrated whether there was a continuous manipulation effect and whether this effect was linear or curved.
- A complex starting model followed by model simplification through stepwise elimination of non-significant independent variables.

Flight time, or number of strings hit, were used as the dependent variables in all models. Sex, date, and breeding location were categorical independent variables. Various morphological variables—mean wing length, head and bill length, body mass, mean original streamer length, and mid tail length were used as continuous independent variables. Also included in the complex starting models was a simple estimate of absolute asymmetry calculated as (absolute value of right tail feather—left tail feather). Absolute asymmetry is used in preference to relative asymmetry as the latter introduces the effect of feather length which is already in the analysis as a covariate. As birds were allocated randomly to treatment groups there should not be any systematic bias due to the effect of asymmetry on manipulated tail length. The flight time data were $\log_{10}$ transformed to fulfill the assumption of normality and the residuals of the fitted models were checked for normality and homoscedasticity after each step.

The table of coefficients from the final ANOVA model was used to produce the equation of any curvilinear relationship between maneuverability and manipulation. The minimum of this curve was estimated by differentiating this equation and setting the first order differential to zero. The solution of the resulting equation gives the manipulation at which maneuverability is maximized. Bootstrapping was used to generate a population of 1000 minima from the original dataset. The 95% confidence intervals were calculated from these data. The final ANOVA model was used in this part of the analysis because it seems more biologically reasonable to allow other sources of variation as well as the manipulation effect into the analysis.

Any experimental birds recaptured during the season were re-released through the maze, allowing a second estimate of maneuverability to be made. This second estimate was used to determine if an individual's performance in the maze differed after a period adjustment to their new tail length using a paired t test.

RESULTS

Swallows

In total, 235 birds were manipulated, of these the time taken to fly through the maze was successfully measured in 84 birds (33 females, 48 males, and three birds could not be sexed). The losses were mainly due to birds flying into the roof or sides of the maze rather than through the stringed section. The number of strings hit was counted in a larger sample of 145 birds. The discrepancy between the sample size for flight time and the sample size for number of strings hit was due to the image of the bird not being visible on the angled mirrors at the ends of the stringed section of the maze. Seventy-nine birds had both flight time and number of strings hit measured. The time taken to fly through the stringed section of the maze was weakly positively correlated with the number of strings hit while doing so ($r = .21$, $p = .06$).

The MANOVA with number of strings hit and $\log_{10}$ flight time had significant effects of both the linear and quadratic manipulation terms ($F_{2,\,76} = 4.21$, $p < .02$; $F_{2,\,76} = 3.97$, $p < .03$ respectively). Flight time was predicted by a categorical manipulation variable ($\mathrm{F}_{6,\,78} = 2.2$, $p < .05$) with the manipulation group −15 mm being significantly lower than the overall mean ($t = -2.45$, $n = 9$, $p = .02$). Using manipulation as a continuous variable flight time was predicted by both the linear and quadratic manipulation terms ($F_{1,\,82} = 7.24$, $p < .01$; $F_{1,\,82} = 6.35$, $p < .02$ respectively). The number of strings hit by the birds as they flew through the stringed section was not significantly predicted by a categorical manipulation variable ($F_{6,\,139} = 0.5$, ns). In addition, the number of strings hit during the flight was not significantly predicted by either the linear or quadratic manipulation terms ($F_{1,\,143} = 0.42$, ns; $F_{1,\,143} = 0.68$, ns, respectively).

The final model explaining individual variation in flight time through the maze after step-wise elimination of the non-significant factors contained the number of strings hit, manipulation and manipulation^2. Both manipulation and manipulation^2 were highly significant in this final model ($F_{1,\,69} = 9.93$, $p < .005$; $F_{1,\,69} = 8.08$, $p < .01$), and the manipulation variable explained 77.4% of the total variation. None of the morphological measures made, date or breeding location were found to explain significant variation in the model and were removed during model simplification. Using the same approach with the number of strings hit as the dependent variable no significant predictors were found.

These analyses all contained a quadratic manipulation term, showing that the relationship between flight time through the maze and manipulation had a curvilinear relationship with a turning point. Differentiation of the ANOVA equation of this curve with respect to manipulation shows this turning point to be a minimum occurring at a manipulation of −12.45 mm. The only difference between the final result of model simplification of the complex ANOVA and the simple single factor ANOVA is the string hit variable. If the equation derived from the simple ANOVA is differentiated this suggests that the minimum occurs at −11.95 mm.

Bootstrapping was used to create 95% confidence intervals around the position of the turning point. The 95% confidence interval for the turning point of the more complex ANOVA was found to be −9.97 mm to −19.00 mm with a median of −12.24 mm.

Therefore, there is a U-shaped relationship between manipulation and flight time through the maze with birds flying fastest and therefore showing most maneuverability with a 12 mm reduction in streamer length (Figure1).

The sex of the bird did not explain significant variance in any of the models. Consequently the type of relationship and the position of the turning point was not significantly different between males and females.

A second estimate of flight time through the maze was made approximately five weeks after manipulation for 12 birds. Using a paired t-test no significant difference was found in individual flight time through the maze immediately after manipulation compared to flight time after a period of adjustment to the new tail length ($t_{11} = 0.89$, $p = .394$). Unfortunately the sample of birds caught several weeks after manipulation was small, ($n = 12$), giving the test a low power (power = 15%). However, the minimum discriminable difference, was calculated (1.47 s), and was of sufficient magnitude to have been detected by our apparatus.

Sand martins

Fifty-seven birds were manipulated, the time taken to fly through the maze was successfully measured in all birds (17 females, 10 males while the remainder could not be sexed). The time taken to fly through the stringed section of the maze was positively correlated with the number of strings hit while doing so ($r = .32$, $p < .02$).

The MANOVA with number of strings hit and $\log_{10}$ flight time had a significant effect of the linear manipulation term

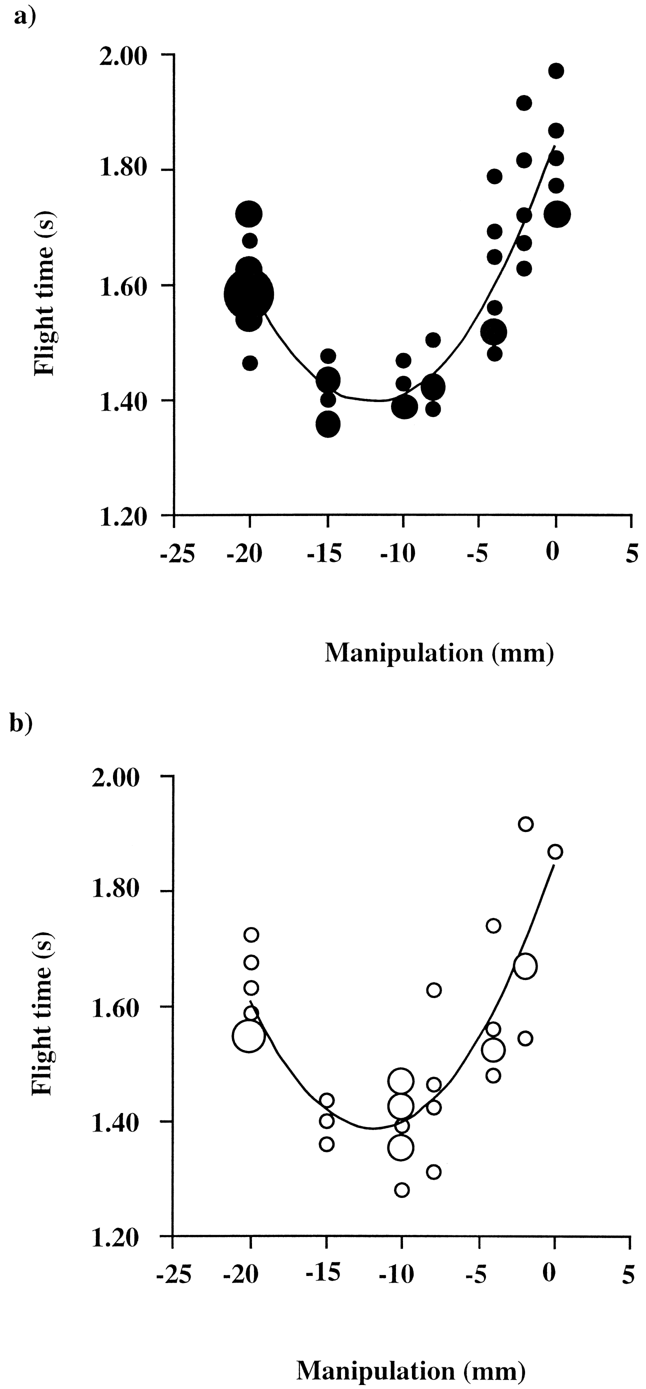

Figure 1
Illustrating the relationship between time taken to fly through the maze for: (a) male and (b) female barn swallows with different amounts of streamer reduction. The time taken to fly through the flight maze is a standardized measure of maneuverability. Point size reflects the number of coincident observations.

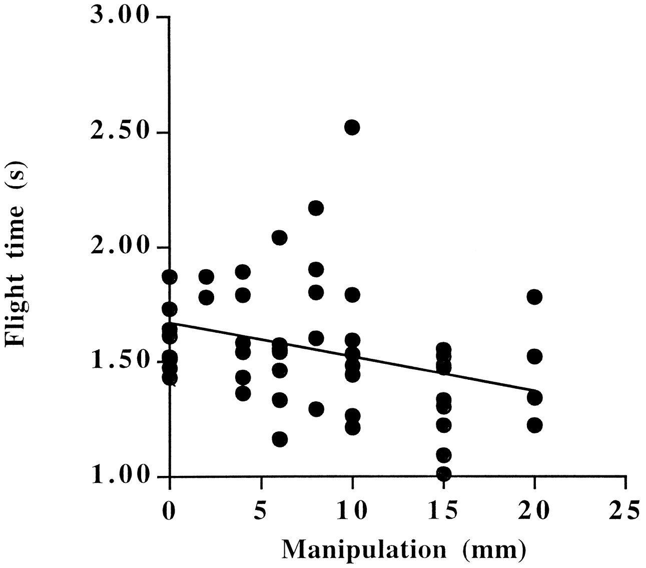

Figure 2
Illustrating the effect of time taken to fly through the maze for sand martins with artificial streamers of differing lengths. Flight time through the maze decreased with increasing elongation.

($F_{2,39}$ = 4.95, $p < .02$) but only when the date of capture was entered in the analysis. If the date effect is not entered then manipulation is not significant ($F_{2,54}$ = 0.91, ns). When analyzed individually the time taken to fly through the stringed section was not predicted by either a categorical manipulation variable ($F_{8,48}$ = 1.24, ns) or a continuous linear manipulation term ($F_{1,55}$ = 1.67, ns). The number of strings hit during the flight was significantly predicted by a categorical manipulation variable ($F_{8,48}$ = 2.8, $p < .02$) but not significantly predicted by a continuous manipulation variable ($F_{1,55}$ = 0.00, ns).

The final model explaining individual variation in flight time through the maze after step-wise elimination of the nonsignificant factors contained the number of strings hit ($F_{6,34}$ = 2.28, $p < .06$), manipulation ($F_{1,34}$ = 7.18, $p < .01$) and date ($F_{15,34}$ = 3.28, $p < .005$). None of the morphological measures made, or breeding location were found to explain significant variation in the model and were removed during model simplification. There were no significant predictors found for the number of strings hit, apart from flight time, which was already shown to be related to the number of strings hit.

Therefore, the data suggests that maneuverability increased with increasing elongation in a linear fashion (see Figure 2).

DISCUSSION

The role of the tail streamer in aerodynamic maneuverability has recently been much in dispute (Evans, 1998, 1999; Hedenström and Møller, 1999). The understanding of such mechanisms is vital before any conclusions can be drawn concerning the evolution of sexual ornaments and cost-reducing traits. The results from this study attempt to do this by quantifying the extent to which maneuverability has shaped the tail streamer. Reduction in barn swallow streamer length was found to increase maneuverability with the initial reduction, while the complex ANOVA analysis demonstrated that maneuverability was maximized at a reduction of 12 mm below natural streamer length. Further reduction in tail length beyond this point caused a decrease in maneuverability, as measured by the flight maze (Figure 1). Referring back to the evolutionary hypotheses, the last 12 mm of the streamer are costly to the bird in terms of decreased flight performance and so are likely to have evolved through sexual selection. In contrast the remainder of the streamer appears to aid maneuverability. The 95% confidence intervals suggest that the true position of the turning point is between −10 and −19 mm. In this study the mean male outer tail feather length was 105.49 ± 9.02 mm and mean female outer tail feather length was 89.55 ± 5.44 mm. This means that the sexually selected component of the outer tail feather length is 9.5%–18% in males and 11%–21.2% in females. This figure will be higher if only the sexually selected streamer is considered, the streamer is approximately 46 mm shorter than the outer tail feather, this means that the sexually selected component of the length of the streamer is about 20% in males and 28% in females. This is consistent with the findings of Buchanan and Evans (2000), suggesting that the majority of the streamer has evolved under natural selection.

Furthermore, our results show that the addition of artificial streamers onto a species that lacks a streamer enhances maneuverability even at short streamer lengths. To our knowledge this is the first time a natural selection advantage has been shown for exaggeration of a trait in a species that does not possess the trait. In terms of streamer evolution, the results suggest a natural selection advantage to possessing even short streamers in terms of enhanced maneuverability. Therefore, the most parsimonious interpretation is that the tail streamer of the barn swallow originally evolved through natural selection, however, the streamer has been elongated beyond the aerodynamic optimum length by sexual selection.

A number of studies have demonstrated the importance of sexual selection in the evolution of the tail of the barn swallow (reviewed in Møller, 1994). Male mating success has been shown to be positively correlated with tail length (Møller, 1990b, 1994); and the tail streamer is assumed to have evolved as a condition-indicator mechanism (Andersson, 1994), signaling parasite resistance and immunocompetence (Møller, 1991a; Møller et al., 1998; Saino et al., 1995). Furthermore such signals appear to have a genetic basis (Møller, 1990b; Saino et al., 1997).

Our results do not directly contradict those of Møller and co-workers or those of Smith and Montgomerie (1991) as we have also found a sexually selected component to the tail streamer. However, by using a series of small manipulations we have been able quantify this and compare its size to the aerodynamically functional part to the tail streamer. Our manipulations have shown that the degree of streamer shortening which produced maximum maneuverability to be around 12mm for swallows. We suggest that this represents the length of the streamer which is sexually selected beyond the aerodynamic optimum. This is of particular relevance to many studies which have used manipulations which are considerably longer than this, (see Møller, 1994 for review), as such manipulations would interfere with the aerodynamically functional part of the tail (Evans and Thomas, 1997; Thomas and Rowe, 1997). Studies of mate choice using experimentally shortened streamers (see Møller, 1994 for review), may be confounded by the fact the males with significantly shortened tails are likely to have altered flight performance. However, it is worth noting that −20 mm manipulations appear to cause somewhat less of a handicap, in terms of flight speed through the maze, than do their original unmanipulated tails (Figure 1) or the elongated tails with a +20 mm manipulation. It is interesting that Møller et al. (1995) found that males given elongated tails caught smaller prey than control males and that males with shortened tails caught larger prey than controls. This is entirely consistent with our results as the males whose tails were shortened by 20 mm will be much closer to the aerodynamic optimum than either control or elongated tail males. We would predict that males whose tails were shortened by about 12 mm would return with larger prey than more extreme reduction manipulations.

Another difference between the mate choice experiments in swallows (Møller, 1994) and this study (and that of Buchanan and Evans, 2000) is that the mate choice experiments used a manipulation of the basal part of the feather while we have manipulated the sexually dimorphic streamer. Thomas and Rowe (1997) argued that the basal manipulation will have large aerodynamic effects as it will alter the aerodynamic properties of the tail surface. Such manipulations will also leave the sexually dimorphic section of the tail unaltered in size, although it will be shifted relative to the bird's body (Thomas and Rowe, 1997). Barbosa and Møller (1999) dismissed these arguments suggesting that manipulations of the "proximal part of the feather does modify streamer length by deplacing [*sic*] it forward or backward." While Barbosa and Møller (1999) could be right if moving the streamer relative to the body effectively changed its size, it is clearly preferable to manipulate directly the part of the feather the selective advantage of which is under consideration. The only study to compare basal manipulations with streamer manipulations, Evans (1998) found that birds with basally manipulated tail feathers differed significantly in flight performance from birds with manipulated streamers. However, the effect of the size of the manipulation was also different between the two types of manipulation (Evans, 1998). This would seem to support the arguments of Thomas and Rowe (1997) rather than Barbosa and Møller (1999).

If streamers are beneficial, why have they not evolved in sand martins? Sand martins like swallows are aerial insectivores, so maneuverability is imperative for foraging success. However, sand martins take smaller, less maneuverable prey items than swallows (Cramp, 1988), therefore they may not require the increased maneuverability offered by a streamer. Although the presence of a streamer aids maneuvering flight, it will be costly during level flight due to drag production. Swallows may be able to compensate for this increase in drag by having larger wings. The smaller wings of sand martins may not generate sufficient lift to compensate for the increased drag a streamer would produce, and this may be a possible constraint on streamer development in sand martins.

Unlike swallows, sand martins nest within burrows in sandy banks. The constant passage through these burrows during a breeding season can cause considerable wear on the feathers and so any adornment is likely to become damaged or broken. A damaged or broken streamer could be worse than no streamer as asymmetry decreases maneuverability (Evans et al., 1994; Møller, 1991b; Swaddle et al., 1996; Thomas, 1993b). Swallows are sexually dimorphic in tail length, with males possessing longer streamers than females (Møller, 1994). This difference has been used to support the sexual selection argument that tail elongation has arisen through female choice (Møller, 1994). However, this sexual dimorphism could be due to a differential risk of damage between the two sexes during incubation, with the risk of damaging a streamer being higher in females as only females of the European race incubate (Smith and Montgomerie, 1991). The fact that males of the North American race incubate and have shorter streamers than their European counterparts (Smith and Montgomerie, 1991) supports this idea. So it would seem that although the presence of a streamer in sand martins aids maneuverability, the cost of a streamer is high enough to prevent feather elongation.

A recent study, Matyjasiak et al. (1999), also measured the effect of giving artificial streamers to sand martins. They found that the addition of tail streamers impaired foraging efficiency as measured by nestling feeding rates and bolus size and composition. However, the experimental protocol used in their study was different from the one employed here, as Matyjasiak et al. (1999) used barn swallow feathers for their manipulations, which may differ in their elastic properties compared to the sand martin feather used in this study. Secondly, our study directly measures the impact of the artificial streamers on flight performance. This may or may not translate directly into changes in foraging success. There are probably various niches available for aerial insectivores, sand martins may have evolved to fill one that has a lower requirement for maneuverability than does the niche occupied by the barn swallow. For the sand martin therefore, increasing maneuverability may not directly increase their foraging success with the foraging strategies employed and the prey species currently taken.

This study looks at the effect of a streamer on flight maneuverability. It does not test for a pre-existing female preference for a tail streamer in the sand martin. A follow up study to determine if female sand martins would select for streamers in this species if they were present, is needed to determine if there is a possibility that the streamer may have been initiated through a combination of female preference and selection for enhanced flight performance.

Surprisingly the sex of the bird had no effect in either model and we found that females showed a similar relationship between streamer shortening and aerodynamic performance as males. It seems likely therefore that female swallows have streamers longer than their optimum under natural selection. Female streamers may have been elongated due to a genetic correlation with the male trait (Møller, 1993), whereby selection in one sex becomes associated with development of the trait in the other. As female tail length appears to be linked to reproductive success, there is some evidence in support of a sexually selected component to the female tail streamer (Møller, 1993). Assortative mating also occurs, with long tailed females more likely to pair with long tailed males (Møller, 1993). Therefore, with the possibility of mutual mate choice, the female tail streamer may also act as a signal of quality, with individuals of higher quality able to carry the cost of more elongated streamers. The fact that there was no difference between males and females in the extent to which the streamer is elongated beyond the aerodynamic optimum, suggests that the sexual dimorphism seen in this species may not be explained by differences in sexual selection.

In contrast to earlier results examining the effect of streamer reductions on flight performance in the barn swallow (Buchanan and Evans, 2000), this study found that initial tail length did not explain significant variation in how the manipulation affected maneuverability. We believe this is explicable as escape from the flight maze presumably involves a number of different components of flight performance, for which both initial tail length and manipulation vary in importance. We can only conclude therefore, that although this study did not find any effect of initial tail length, we cannot discount the fact that such an effect may have been obscured by varying effects of tail length on different aspects of flight.

According to delta wing theory (Thomas, 1993a), the area of tail in front of the point of maximum continuous span of the tail produces lift and any area behind it generates drag. Therefore, delta wing theory suggests that streamers are drag producing structures. However, by drooping the outer tail feathers to form leading edge suction, the induced drag from the added streamers may be substantially reduced (Thomas, 1993a). In addition, the streamers may enhance maneuverability by increasing drag as turn radius is inversely proportional to drag. A third possibility is that the addition of these short streamers has lengthened the maximum continuous span. If the distal edge of the tail was curved when fully spread, then the addition of the streamers on the outer tail feathers would increase maximum continuous span by a small amount. This would function to increase lift and hence maneuverability. Therefore, while we have evidence for a natural selection advantage to the streamer, the mechanism through which it is functioning remains to be determined.

The exact mechanism enhancing maneuverability cannot be determined from this experiment, although, it is plausible that it is consistent with a mechanism similar to that proposed by Norberg (1994). This theory, however, relies on the flexibility of the outer tail feather and its ability to rotate within the socket. It also needs the outer tail feather to produce a pitching moment which in turn causes the formation of a drooped leading edge. The streamer may need to be above a threshold size before it can generate a sufficient pitching moment to form a drooped leading edge. Therefore, the Norberg mechanism may only function at long streamer lengths where the streamer is able to twist and bend in the airflow.

As the artificial streamers added to the sand martins involved the addition of a new section onto the outer tail feather, the elastic twisting mechanism of the feather will be different from that of a continuous feather of the same length. Also, it is not known if the outer tail feathers of sand martins are able to rotate in a similar manner to those of a swallow. Therefore, while the artificial streamers added to the sand martins and the tail streamers of the barn swallow were both found to enhance maneuverability, we are unable to determine if they are acting through the same mechanism.

This study considers the costs and benefits of possessing tail streamers during turning flight. During non-turning flight the tail is furled, therefore, it is probable that the streamer will have a different effect in level flight and that the costs and benefits of a streamer will change under these conditions. The relative costs and benefits of elongated streamers in relation to flight performance must influence their evolution for individuals and is likely to be determined by the relative importance of different types of flight. The cost of a streamer during level flight due to increased drag may be important as it will increase the energetic demands of straight flight during migration. Studies of hematocrit after migration have found higher levels in long tailed males, implying these males to have a higher activity level during migration (Saino et al., 1997). Closer examination of how and when the Norberg mechanism is operating is essential for understanding how it effects flight efficiency.

This is the first time a tail streamer has been to shown to benefit flight performance in a species without a streamer. These results show that elongation of the outer tail feather into a streamer enhances maneuverability even at short lengths. This would allow natural selection to select for a streamer at the onset of initial feather elongation. Without any conclusive evidence to the contrary it would seem most likely that the tail streamer of the swallow evolved initially through a natural selection pressure for increased maneuverability, not through sexual selection pressures. This is in contrast to the conclusions of Møller and Hedenström (1999) that the tail streamer was initially selected for by sexual selection and only later became important for aerodynamics. We suggest that subtle changes in ecology, either in foraging ecology selecting for increased maneuverability or in breeding ecology lowering the cost of streamer damage could rapidly result in streamers evolving in aerial foragers. We would predict that given such changes in ecology streamers could evolve rapidly through natural selection, it may be possible to test this by comparing the maneuverability in flight of species with streamers and closely related streamer-less species.

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