

## ORIGINAL ARTICLE

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## Assessing the aerodynamic effects of tail elongations in the house martin (*Delichon urbica*): implications for the initial selection pressures in hirundines

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**Abstract** Of the three species of hirundine that breed sympatrically across the U.K., one, the barn swallow, has outer tail feathers elongated into streamers, whereas the other two species, the house martin and the sand martin, do not. The tail streamer of the barn swallow is regarded as a classic example of a sexually selected trait. Recent evidence, however, has suggested that streamers may have evolved largely through natural selection for enhanced flight performance and increased maneuverability. We tested the hypotheses that small streamers (1) increase performance in turning flight, but (2) decrease performance in flight variables related to velocity. We manipulated the lengths of house martin outer tail feathers and measured changes in their free-flight performance, using stereo-video to reconstruct the birds' three-dimensional flight paths. Five flight variables were found to best describe individual variation in flight performance. Of these five, the three variables determining maneuverability predicted that flight performance would be optimized by a 6- to 10-mm increase in the length of the outer tail feathers. In contrast, for mean velocity and mean acceleration, extension of the outer tail feathers appears to have a detrimental effect on flight performance. We suggest that the initial selection pressure for streamers in ancestral short-tailed 'barn swallows' was via natural selection for increased maneuverability. In addition, we propose that the benefits of increased maneuverability have differed between hirundines in the past, such that the cost of increasing the length of the outer tail feather has, to date, outweighed the benefits of doing so in streamerless hirundines.

**Key words** Flight performance · Hirundines · Natural selection · Sexual selection · Tail streamers

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### Introduction

The traits of many animals fulfill several important functions. The assumption is that the current observed size of such traits is the fitness optimum. However, this may not be the optimum for each, or any, of the separate functions of a trait. In addition, some traits would appear to have no survival advantages for the bearer, and Darwin (1871) suggested sexual selection as a mechanism for the development of such traits. In the last 20 years, considerable interest has been paid to the possible trade-offs between natural and sexual selection pressures (Andersson 1994). Avian tail morphology represents a good example of trade-offs between multiple functions, as tails may have several uses (Balmford et al. 1993). Theory predicts that different modes of flight (e.g., migratory flight, foraging flight) would select for different optimal tail designs (Thomas 1995). Tails are also used for signaling and during mate choice, and these functions will produce different selection pressures on the tail than will aerodynamic functions (Balmford et al. 1993).

Many hirundines (Hirundinidae) possess elongated outer tail feathers (streamers). This trait appears to have evolved at least twice (Møller 1994), although the initial evolutionary pressures for streamers are unknown (but see Matyjasiak et al. 2000; Rowe et al., in press). The three species that breed around the study sites used here are sympatric across their range: barn swallows (*Hirundo rustica*) have streamers while house martins (*Delichon urbica*) and sand martins (*Riparia riparia*) do not. Male barn swallows have streamers which are approximately 16% longer than those of females (Møller 1988). Females preferentially mate with males that have long streamers, so long-tailed males benefit from a higher annual reproductive success (Møller 1988; Smith and Montgomerie 1991). The streamer of the male barn swallow has been regarded as a classic example of a secondary sexually selected trait (Møller 1994) since, theoretically, the streamer impairs aerodynamic performance through increased drag (Thomas 1993). Only high-quality males are able to withstand this handicap and for ex-

ample, long-tailed males have been found to have higher survival rates and reduced parasitism levels (Møller 1989; Møller and de Lope 1994). More recently, however, it has been proposed that streamers may, to some extent, aid aerodynamic performance (Norberg 1994). Because of the aeroelastic properties of the outer tail feather, the streamer bends upward and backward to create a vortex flap at the front edge of the tail. This flap helps prevent flow separation, thereby delaying stalling to higher angles of attack and allowing the bird to perform tighter turns, so improving maneuverability (Norberg 1994). To date, the sexual selective advantages of possessing streamers have been extensively studied (Møller 1994), but the aerodynamic effects of such a trait have not (but see Buchanan and Evans 2000).

Evans and Thomas (1997) suggested that the naturally and sexually selected components of the barn swallow's streamer could be distinguished by artificially reducing its length and examining the effect this has on flight costs. If the streamer is at a naturally selected optimum, any shortening should increase flight costs. If the streamer is the product of sexual selection, reducing its length should decrease flight costs. If, however, the streamer is the product of natural selection exaggerated through sexual selection, shortening the streamer progressively should cause an initial decrease in flight costs (as the sexually selected handicap is removed), followed by an increase in costs as the naturally selected component is removed. This would produce a curvilinear relationship between flight costs and the degree of streamer shortening. Buchanan and Evans (2000) found curvilinear relationships between degree of streamer shortening in barn swallows and several different measures of flight performance. By determining the maximum/minimum point of the quadratic function, they concluded that a reduction in streamer length of between 7 and 15 mm would optimize flight performance (Buchanan and Evans 2000). This suggests that streamers are largely the product of natural selection but that sexual selection has been responsible for the extension of the streamers past their aerodynamic optimum.

We can also use aerodynamic theory to predict changes in flight performance after the addition of a small streamer to hirundine species that lack this trait. If the initial selection pressure promoting the evolution of tail streamers was enhanced aerodynamic performance (via natural selection), adding a small streamer should result in an initial increase in flight performance, followed by a decrease after the optimum length is exceeded. If, however, the initial pressure was sexual selection, any increase in the length of the outer tail feather would result in a continuous decrease in flight performance. House and sand martins are ideal subjects for such studies because they do not possess streamers and mate choice is unlikely to be an influencing factor in tail evolution as the tails of males and females are morphologically similar. Presumably then, tail morphology in these species is at its naturally selected optimum. Rowe et al. (in press) found that the addition of small streamers (up to 20 mm)

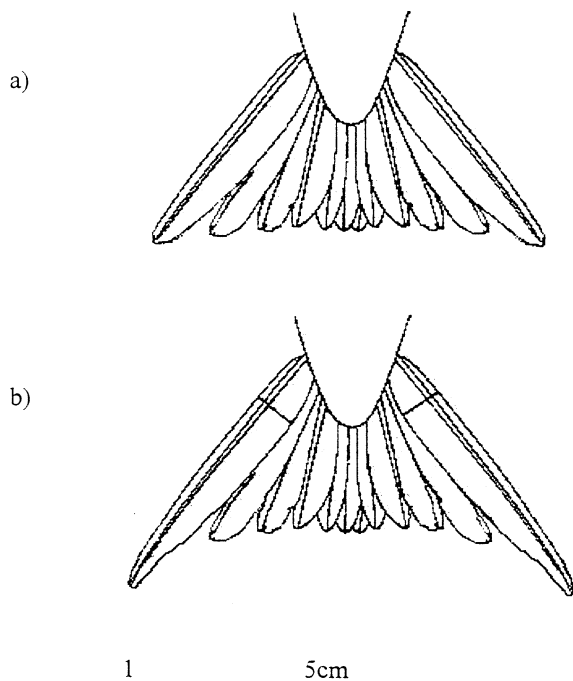
to sand martins increased flight maneuverability, indicating that species without streamers could gain some aerodynamic benefit from the evolution of small streamers. This indicates, as suggested by Norberg (1994), that the initial selection pressure for streamers in the short-tailed ancestor of the barn swallow may have been via natural selection for increased maneuverability. However, whether this is traded off against detrimental effects on flight variables other than maneuverability is not known.

In this study, we attempted to mimic the early stages of streamer evolution by adding small streamers to house martins. Based on results from experimental manipulations of sand martin tails and aerodynamic theory, our central hypothesis is that streamers initially evolved for increased maneuverability, but at the expense of other measures of flight performance. This implies that the relative costs and benefits of streamer evolution differ between barn swallows and the two species of martin. We predict that the addition of streamers to house martins will: (1) produce curvilinear relationships with measures of flight that determine maneuverability (an initial increase in maneuverability, followed by a decrease after the streamer length exceeds the aerodynamic optimum), and (2) produce monotonically decreasing relationships with other measures of flight performance. These results should allow us to ascertain which aspects of flight performance have been instrumental in the evolution of tail morphology, specifically in house martins, but also more generally in hirundines without streamers.

Barn swallows have long been regarded as having greater maneuverability than either house or sand martins (Waugh 1978; Turner and Rose 1989), although the evidence for this has been based largely on casual observations of hirundine flight, their tail design, and the type of insect prey brought back to the nest (Waugh 1978). Maneuverability is defined as the tightest turn (minimum turn radius) of which a bird is capable (Thomas 1996). To date, no direct comparisons of maneuverability between different hirundine species have been made. Our second aim in this study was to test the hypothesis that barn swallows are more maneuverable than house martins at natural outer tail feather lengths. Using commuting flight data collected from unmanipulated barn swallows (from Buchanan and Evans 2000), we compared calculated measures of minimum turn radius to that of unmanipulated house martins in this experiment.

## Methods

Male and female house martins were caught while roosting in artificial nest boxes at two breeding sites in central Scotland in 1998 and 1999. The following biometric measurements were taken; left and right wing length (maximum chord), left and right outer tail feather length, and the length of the mid-tail feather were measured to the nearest millimeter with a ruler; head and bill length was measured to the nearest 0.1 mm using vernier calipers; body mass was measured to the nearest 0.1 g using a pesola spring balance. Paired measurements were averaged to calculate mean wing and outer tail length. Repeatability estimates (intra-class correlation coefficient,  $r_i$ ) for these measurements were calculated



**Fig. 1** Unmanipulated (a) and manipulated (+15 mm) (b) house martin outer tail feathers. Birds in the experimental groups (+6 and +15 mm) had the two outer tail feathers cut to within 10 mm of the base (indicated by the horizontal lines across the feather) and replaced with outer tail feathers from a swallow which were butted onto the feather shaft and fixed by the insertion of a 5-mm wire pin (0.6 mm gauge, <10 mg) into the pulp cavity of the rachis. Cyanoacrylic superglue was used to hold the pin in place. The outer tail feathers were trimmed to give a natural rounded end, and at the side in order that it graduated in accordance with the other tail feathers (i.e., trailing edges overlapped). Care was taken to ensure that the feather vane of the manipulated feather was adjusted during manipulation to lie in the same plane as the tail

(Lessels and Boag 1987) using individuals caught more than once. Mean wing length ( $F_{17,18}=13.60$ ,  $P<0.001$ ,  $r_i=86\%$ ), mean outer tail feather length ( $F_{20,21}=22.81$ ,  $P<0.001$ ,  $r_i=92\%$ ), mid-tail feather length ( $F_{20,21}=5.56$ ,  $P<0.001$ ,  $r_i=69\%$ ), and head and bill length ( $F_{20,21}=3.59$ ,  $P<0.001$ ,  $r_i=56\%$ ) were significantly repeatable. Body mass ( $F_{20,21}=1.98$ , NS,  $r_i=33\%$ ) was not significantly repeatable. Sex was determined by the presence (female) and absence (male) of a brood patch (Svensson 1992). Before release, individuals were marked on the breast and rump with a unique combination of dyes (Pantone Inks, Letraset) so they could be identified in the field.

Marked birds were filmed flying towards and away from nest boxes using two Sony cameras (Sony Digital Handycam DCR-VX1000E) mounted 1 m apart on a rigid bar. The cameras were aligned at  $90^\circ$  to the mounting bar which was held level. The stereo-video technique allows the reconstruction of three-dimensional (3D) flight paths which can be used to calculate various measures of free-flight performance (Evans 1998; Buchanan and Evans 2000; M.R. Evans, K.L. Buchanan, K.J. Park, unpublished data). Once birds had been filmed, they were recaptured and randomly allocated to one of two experimental groups (6- or 15-mm streamer), or a control group (no streamer). Birds in the experimental groups had the two outer tail feathers cut to within 10 mm of the base and replaced with outer tail feathers from a swallow which were butted onto the feather shaft and fixed by the insertion of a 5-mm wire pin (0.6 mm gauge, <10 mg) into the pulp cavity of the rachis (Smith and Montgomerie 1991; Matyjasiak et al. 1999). Cyanoacrylic superglue was used to hold the pin in place. The outer tail feathers were then trimmed to a

natural streamer shape 6 or 15 mm longer than the length of the original tail feather (Fig. 1). Birds in the control group had the same length of wire fixed to the base of the outer tail feathers with cyanoacrylic superglue to control for the weight of the wire. Manipulated birds were then refilmed. Filming took place between 1 and 7 days after manipulation. Multiple flight sequences were obtained for each bird, and an average value for the flight variables before and after manipulation was calculated. These variables will be referred to in the subsequent text as the initial flight variables (before manipulation) and final flight variables (after manipulation).

The stereo-video footage was digitized using the miROMOTION DC20 digitizer (Pinnacle Systems, UK) on an Apple Macintosh 9500. The digitized footage was then edited using Adobe Premiere 4.0 (Adobe Systems) and the 2D co-ordinates of the center of the bird's body (on both the left and right camera) were obtained from each frame using the public domain NIH image program (available on the internet at <http://rsb.info.nih.gov/nih-image/>). The focal length of the camera, camera separation, and the stereo-pairs of 2D co-ordinates were then used by a computer program to obtain the 3D co-ordinates for the flight path. The 3D co-ordinates were smoothed using a fourth-difference algorithm (Rayner and Aldridge 1985), and used to calculate flight variables for individual flight paths: mean, minimum, and maximum velocity; mean, minimum, and maximum acceleration; mean and maximum energy (sum of potential and kinetic); mean and maximum curvature; mean and maximum rate of change of curvature; mean and maximum curvature in the XY plane; mean and maximum rate of change of curvature in the XY plane; mean, minimum, and maximum turn radius; mean and maximum agility. The XY plane represents the vertical 2D plane running parallel to the cameras. For details of how these variables are calculated refer to Rayner and Aldridge (1985), Buchanan and Evans (2000), and M.R. Evans, K.L. Buchanan and K.J. Park (unpublished data). The error (accuracy) associated with these measurements was estimated by plotting the co-ordinates for a stationary object 1 m in length and calculating the error in the positional data which was 8.0% (SE  $\pm 0.51$ ,  $n=207$ ). The errors associated with the calculation of the flight variables are discussed in M.R. Evans, K.L. Buchanan and K.J. Park (unpublished data) and are all under 10%. All filming and digitizing were carried out blind to the manipulation group of the bird being filmed.

Data were transformed to achieve normality and analyzed using MINITAB release 12.1 and SPLUS 4.5. As the 21 flight variables calculated do not vary independently, they were reduced to the smallest set of independent variables that explained significant covariation in the others (see also Buchanan and Evans 2000). Only initial flight variables (i.e., before manipulation) were used for this analysis to avoid considering each bird twice. Mean velocity was found to explain significant variation in the largest number of variables. Flight variables not explained by mean velocity were added to it sequentially and multiple regression was used to find which combination of two variables explained significant variation in the largest number of remaining variables. This process was continued until all the flight variables were explained by the smallest set of independent predictor variables. Five flight variables were found which best explained most individual variation: mean velocity, mean acceleration, maximum curvature, maximum curvature in the XY plane, and maximum rate of change of curvature in the XY plane. Curvature is a scalar measure of the deformation of the flight path, and therefore provides quantitative information on maneuverability. Curvature in the XY plane is a component of this measurement, and is an important measure of performance in a level turn (Rayner and Aldridge 1985). The term performance is used in this paper in relation to an individual's behavioral strategy, and is not intended to infer that particular flight characteristics are more desirable than any other.

We have taken two approaches to the analysis of these data, which differ only in the degree of complexity of the statistical models [general linear model (GLM) ANOVA] constructed:

- (1) A simple model was constructed for each of the five flight variables, with the final flight variable as the dependent variable. Only year, site (factors), the initial flight variable, and the

variable of interest, manipulation and manipulation<sup>2</sup> (covariates), were included in these models. If the quadratic term manipulation<sup>2</sup> did not explain a significant amount of variation in the final flight variable, it was removed in order to assess the importance of the linear-term manipulation to the model.

- (2) A more complex starting model followed by model simplification through stepwise elimination of non-significant independent variables was constructed for each of the five flight variables. Again, the final flight variable was the dependent variable, and the initial flight variable, tail manipulation group, and individual morphological measures were continuous independent variables (covariates). Year, site, and sex were included in the models as factors. Interactions between tail manipulation and sex, the initial flight variable and the average length of the outer tail feathers were also included in the starting models. Year, site, and initial flight variable were constrained into the model regardless of their significance.

The residuals were checked at each stage for a normal distribution and homoscedasticity. The regression coefficients of the complex stepwise GLM were used to produce the equation of the line relating final flight variable to manipulation. Where a curvilinear relationship was found between final flight variable and manipulation, the maximum/minimum point was determined by differentiation of the regression coefficients. The maximum/minimum point on a curve can be defined as  $df/dx=0$ , that is the manipulation size at

which the rate of change of the function becomes zero. Using bootstrapping, a population of maximum/minimum points was generated from the original dataset allowing estimation of the 95% confidence intervals and interquartile ranges.

For a comparison of maneuverability between barn swallows and house martins, the minimum turn radius of unmanipulated barn swallows (from Buchanan and Evans 2000) filmed using the same equipment and analyzed using the same technique was compared to that of unmanipulated house martins under similar flight conditions (commuting flight: flying towards and away from nest sites).

## Results

Flight sequences before and after manipulation were obtained for 16 house martins. Repeatability estimates of final flight variables were calculated from between 3 and 21 flight sequences for the same individual ( $n=16$ ). The  $r_i$  values are presented alongside  $F$ -ratios and  $P$ -values calculated in the ANOVA. Most flight variables were significantly more variable between than within individuals. Mean velocity ( $F_{15,99}=24.35$ ,  $P<0.001$ ,  $r_i=77%$ ), mean acceleration ( $F_{15,101}=1.94$ ,  $P<0.05$ ,  $r_i=12%$ ), maximum

**Table 1** Results from the simple general linear models for each flight variable examined. Effects of streamer addition (manipulation and manipulation<sup>2</sup>), initial flight variable, site, and year are shown. If the quadratic term manipulation<sup>2</sup> did not explain a sig-

nificant amount of variation in the final flight variable, it was removed in order to assess the importance of the linear-term manipulation to the model (\* $P<0.05$ , \*\* $P<0.01$ )

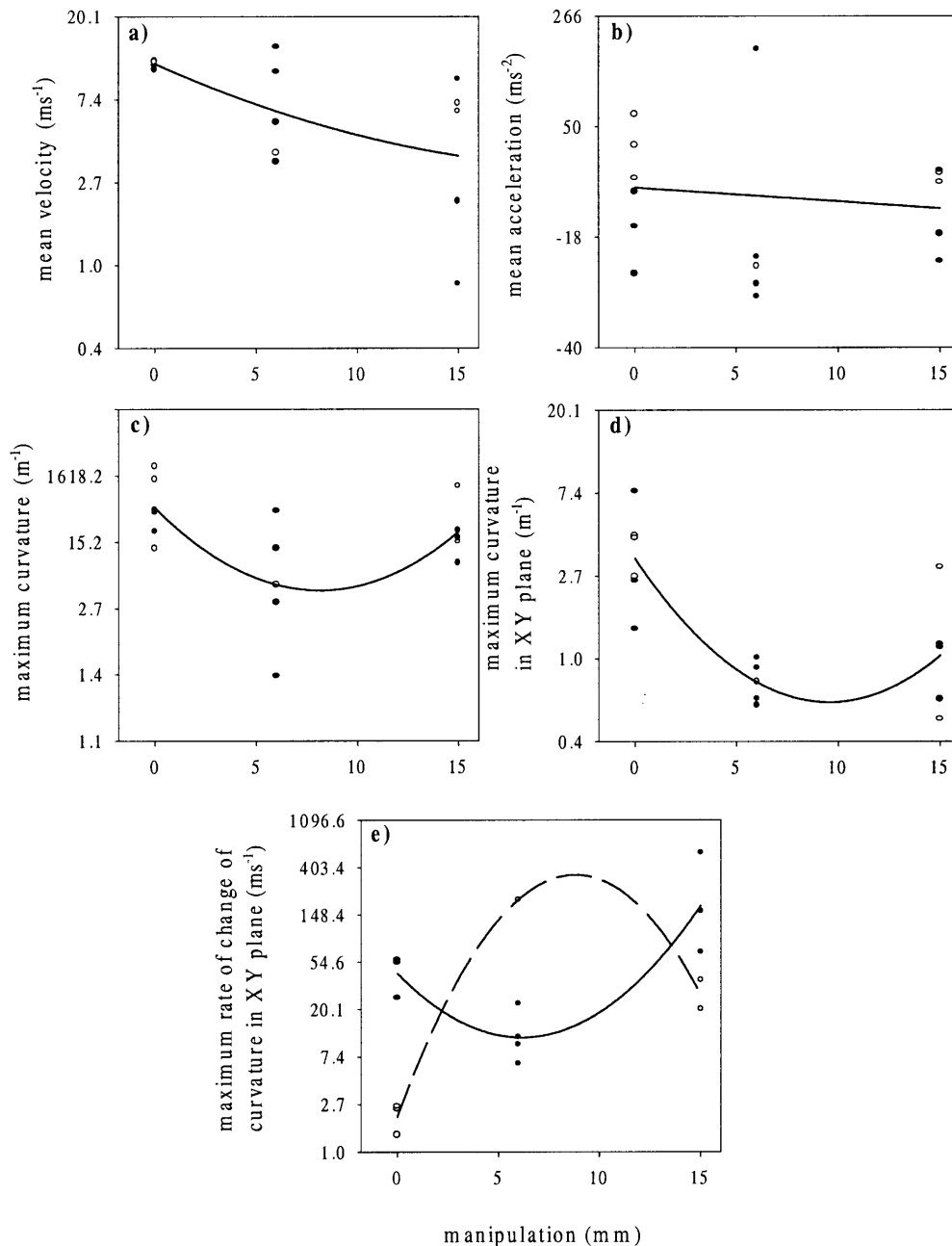
	Mean velocity	Mean acceleration	Maximum curvature	Maximum XY curvature	Maximum rate of change of XY curvature
Year	$F_{1,11}=5.39^*$	$F_{1,11}=3.91$	$F_{1,10}=0.72$	$F_{1,10}=10.31^{**}$	$F_{1,10}=0.14$
Site	$F_{1,11}=4.57$	$F_{1,11}=9.31^*$	$F_{1,10}=0.98$	$F_{1,10}=10.02^{**}$	$F_{1,10}=13.41^{**}$
Initial variable	$F_{1,11}=0.01$	$F_{1,11}=0.00$	$F_{1,10}=0.04$	$F_{1,10}=0.39$	$F_{1,10}=0.02$
Manipulation	$F_{1,11}=5.42^*$	$F_{1,11}=4.64^*$	$F_{1,10}=4.64$	$F_{1,10}=12.10^{**}$	$F_{1,10}=8.04^*$
Manipulation <sup>2</sup>	–	–	$F_{1,10}=4.96^*$	$F_{1,10}=8.89^*$	$F_{1,10}=5.96^*$

**Table 2** Results from the complex general linear models for each flight variable examined. Effects of streamer addition (manipulation and manipulation<sup>2</sup>), initial flight variable, sex, site, year, the interaction terms, and morphological variables on individual vari-

ation in the final flight variable are shown. Initial flight variable, site, and year were all constrained into the models and do not always have a significant effect (\* $P<0.05$ , \*\* $P<0.01$ )

	Final mean velocity	Final mean acceleration	Final maximum curvature	Final maximum curvature in XY plane	Final maximum rate of change of curvature in XY plane
Manipulation	$F_{1,4}=52.97^{**}$	$F_{1,9}=10.65^*$	$F_{1,10}=4.64^*$	$F_{1,10}=12.10^{**}$	$F_{1,6}=1.14$
Manipulation <sup>2</sup>	$F_{1,4}=41.80^{**}$		$F_{1,10}=4.96^*$	$F_{1,10}=8.89^*$	$F_{1,6}=0.75$
Initial flight variable	$F_{1,4}=50.43^{**}$	$F_{1,9}=3.13$	$F_{1,10}=0.04$	$F_{1,10}=0.39$	$F_{1,6}=8.27^*$
Sex					$F_{1,6}=8.34^*$
Site	$F_{1,4}=93.16^{**}$	$F_{1,9}=3.90$	$F_{1,10}=0.98$	$F_{1,10}=10.02^*$	$F_{1,6}=4.68$
Year	$F_{1,4}=80.29^{**}$	$F_{1,9}=5.26^*$	$F_{1,10}=0.72$	$F_{1,10}=10.31^{**}$	$F_{1,6}=3.82$
Interaction terms					
Mean outer tail length (manipulation)	$F_{1,4}=44.92^{**}$	$F_{1,2}=10.30^*$			
Initial flight variable (manipulation)	$F_{1,4}=49.04^{**}$				
Sex(manipulation)					$F_{1,6}=7.17^*$
Sex(manipulation <sup>2</sup> )					$F_{1,6}=6.00^*$
Morphological variables					
Mean wing length	$F_{1,4}=30.83^{**}$				$F_{1,6}=9.56^*$
Mean tail length	$F_{1,4}=72.10^{**}$	$F_{1,9}=6.49^*$			
Head and bill	$F_{1,4}=19.42^*$				
Final mass	$F_{1,4}=21.2^*$				

**Fig. 2** The relationships for males (*closed circles*) and females (*open circles*) between tail manipulation and mean velocity (a), mean acceleration (b), maximum curvature (c), maximum curvature in the XY plane (d), and maximum rate of change of curvature in the XY plane (e) [ $n=16$  birds:  $n=6$  (control group),  $n=5$  (+6-mm manipulation),  $n=5$  (+15-mm manipulation) for all flight variables]. Transformed data are plotted controlling for all effects in the model except manipulation, and the regression lines indicate the effect of manipulation on each flight variable. Values on the y-axis of each graph have been back-transformed according to the transformation initially performed on each flight variable. The maximum/minimum point of 9.78 mm for mean velocity is not obvious (a), in part because the curved relationship between manipulation and velocity is extremely shallow and could essentially be considered linear. In addition, there is a significant interaction between manipulation and original outer tail feather length (Table 2). This interaction indicates that for each length of tail there is a different slope which best describes the relationship between manipulation and the flight variable. The mean velocity data represent the effect of tail manipulation on an average tail length of 60.87 mm. For maximum rate of change of curvature in the XY plane, sex interacted significantly with the effect of tail manipulation. For this variable only, the regression lines are plotted separately for each sex (*solid line* males, *dashed line* females)



curvature ( $F_{15,101}=3.42$ ,  $P<0.001$ ,  $r_i=25\%$ ), maximum curvature in the XY plane ( $F_{15,98}=2.46$ ,  $P<0.01$ ,  $r_i=17\%$ ), and maximum rate of change of curvature in the XY plane ( $F_{15,97}=2.85$ ,  $P=0.001$ ,  $r_i=21\%$ ) were all significantly repeatable.

#### Relationship between flight performance and addition of streamers

Results from the simple GLMs (Table 1) show that maximum curvature, maximum curvature in the XY plane, and maximum rate of change of curvature in the XY plane all had significant curvilinear relationships with tail manipu-

lation. In contrast, the relationship between mean velocity and mean acceleration with manipulation was best described with a negative linear function. The complex models, containing sex, morphological variables, and interactions, show a similar pattern: of the five independent flight variables, four were found to have significant curvilinear relationships with tail manipulation, either alone (mean velocity, maximum curvature, maximum curvature in the XY plane) or in an interaction with sex (maximum rate of change of curvature in the XY plane) (Fig. 2, Table 2). The fifth independent flight variable – mean acceleration – had a negative linear relationship with tail manipulation. All results presented from here on relate to those derived from the complex models.

**Table 3** Position of the maximum/minimum (mm) for each flight variable with a significant manipulation<sup>2</sup> term (quadratic function), calculated from the ANOVA coefficients, and the distribu-

tion of turning points derived from bootstrapping showing the median, upper and lower 95% confidence intervals, and upper and lower quartiles

	Mean velocity	Maximum curvature	Maximum curvature in XY plane	Maximum rate of change of curvature in XY plane	
				Female	Male
Position of the turning point (mm) calculated from ANOVA	9.78	8.14	9.56	8.80	6.16
Distribution of the turning point derived by bootstrapping					
95% upper confidence	-1,023.83	-0.04	-0.02	-1.07	-2.83
Upper quartile	-120.33	6.25	7.50	-0.01	-0.08
Median	15.00	7.50	8.75	0.84	0.17
Lower quartile	88.50	8.75	10.25	1.69	2.02
5% lower confidence	1,288.50	11.50	15.00	11.25	11.50

**Table 4** Effect of the manipulation<sup>2</sup> term (quadratic function) on the  $R^2$  (variance explained) of the final model. The  $R^2$  of the model before and after the removal of the quadratic function is shown

along with the percentage reduction in  $R^2$  (and the  $P$ -value for the size of the absolute reduction in  $R^2$ )

	Mean velocity	Mean acceleration	Maximum curvature	Maximum curvature in XY plane	Maximum rate of change of curvature in XY plane
Model $R^2$	99.29	81.50	53.17	80.67	89.23
Model excluding manipulation <sup>2</sup> $R^2$	91.82	81.50	29.93	63.47	77.12
Percent reduction in $R^2$	7.52	0	43.70	21.31	13.58
	0.5> $P$ >0.25		0.05> $P$ >0.025	0.1> $P$ >0.05	0.2> $P$ >0.1

To determine the optimal streamer length for each flight variable showing a curvilinear relationship with tail manipulation, the position of the maximum/minimum point was calculated using the regression coefficients from the models (Table 3). The maximum/minimum points for all four quadratic relations were greater than zero and ranged from 6.16 to 9.78 mm (Table 3). The maximum/minimum point for mean velocity was 9.78 mm although this is not obvious from Fig. 2a, in part due to the significant interaction between manipulation and outer tail feather length (Table 2). The interaction indicates that the effect of tail manipulation varies with the original length of the outer tail feather. The data in Fig. 2a represent the effect of tail manipulation on velocity with an average tail length of 60.87 mm. Data from the GLMs were used to calculate a population distribution of maximum/minimum points using bootstrapping (1,000 replicates) (Table 3). Confidence intervals (upper and lower 95%) and interquartile ranges (25% and 75%) were calculated. Confidence intervals describing the optimum outer tail feather length for mean velocity were extremely wide, with values exceeding  $\pm 1,000$  mm (Table 3). This is explicable as the relationship between mean velocity and manipulation is virtually linear: the percentage of replicates for mean velocity with maximum/minimum points between 0 and 20 mm (a range which we consider represents a 'small streamer') was very low (5%). This indicates that the curve for the effect of manipulation on mean velocity is extremely shallow. In contrast, confidence intervals for the mea-

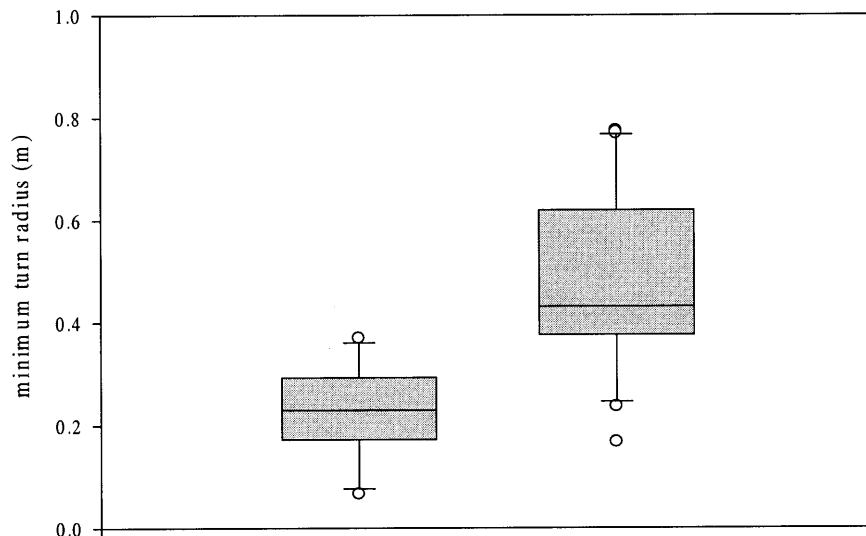
asures of curvature were considerably tighter than this and ranged from -2.83 to +15.00 mm (Table 3). The percentage of replicates with maximum/minimum points between 0 and 20 mm was far higher than for mean velocity: maximum curvature (89%), maximum curvature in the XY plane (89%), and maximum rate of change of curvature (female=70%, male=64%).

The influence of the quadratic (manipulation<sup>2</sup>) term upon the flight variables can be illustrated by comparing the  $R^2$  (proportion of variance explained) of each model with and without the quadratic term (Table 4). The percentage change in  $R^2$  caused by the removal of the quadratic term is small for mean velocity (7%). However, the quadratic term has a larger effect on maximum curvature, maximum curvature in the XY plane, and rate of change of curvature in the XY plane, as its removal results in a reduction of  $R^2$  by 56%, 16%, and 13%, respectively. Again, this indicates that, in contrast to the curves from the other flight variables, the curve for the effect of manipulation on mean velocity is extremely shallow.

#### Comparison of maneuverability between barn swallows and house martins

The comparison of barn swallow turning flight with that of unmanipulated house martins under similar conditions showed that barn swallows had significantly smaller turn radii than house martins, that is, they performed tighter turns in flight than did house martins ( $t$ -test,  $T_{6,16}=3.96$ ,  $P<0.01$ ; Fig. 3).

**Fig. 3** Comparison of minimum turn radius (commuting flights) between unmanipulated barn swallows ( $n=10$ ) (left) and house martins ( $n=16$ ) (right). Box plots shown here indicate the 10th, 25th, 50th, 75th, and 90th percentiles with *horizontal lines* and all data points outside this range



## Discussion

### Impact of streamers on flight performance

Both the simple and the complex models presented for this study show, as predicted, curvilinear relationships for flight variables determining maneuverability (maximum curvature, maximum curvature in the XY plane, and maximum rate of change of curvature in the XY plane). This experiment has shown that the flight performance of house martins during turning flight is optimized by a 6- to 10-mm increase in the length of the outer tail feathers. This demonstrates that flight performance in turning flight increases with the addition of a small streamer up to an optimal length, and then decreases once the optimal length has been exceeded. Due to the wide confidence intervals, the exact position of the optimal streamer length for maneuverability is unclear (Table 3), possibly in part due to the small sample size of this study. However, the high percentage of replicates that had an optimum between 0–20 mm indicates the high probability that the aerodynamic optimum for maneuverability in house martin tails lies within this region.

The position of the maximum/minimum point on a quadratic function can either be the minimum point of a U-shaped curve, or the maximum point of an n-shaped curve (Evans and Thomas 1997). Examination of the maximum rate of change of curvature in the XY plane showed that there were differences between males and females in the form of the quadratic function, with males displaying a U-shaped response to manipulation, and females an n-shaped response. The position of the maximum/minimum point was, however, very similar (6.2 and 8.8 mm, respectively). The reason for these differences is unclear, but it should be stressed that the sample sizes involved in a comparison of the sexes were very small, and more data are required if this result is to be interpreted with any confidence.

Mean velocity and mean acceleration had negative linear relationships with manipulation (simple model), but there was a significant curvilinear relationship of mean velocity with manipulation in the complex model. In this model, however, the wide confidence intervals, low percentage of replicates with a maximum/minimum point between 0 and 20 mm, and the low  $R^2$  of the quadratic term indicate that although there was a significant quadratic relationship between mean velocity and tail manipulation, the curve is extremely shallow and probably of limited biological significance. The relationship between mean velocity and manipulation, therefore, could essentially be considered a negative linear one, mean velocity decreasing with manipulation size over the region of interest. The decrease in velocity and acceleration with the addition of small streamers is consistent with models of minimum power and maximum range speed changes for scarlet-tufted malachite sunbirds with elongated tails (Evans and Thomas 1992). Whether this decrease in velocity and acceleration can necessarily be interpreted as detrimental to the bird's flight is not obvious. The alternative is that this decrease is beneficial to the bird's flight but that the optimum length of streamer exceeds the maximum manipulation used here (15 mm). We believe, however, that adding a streamer of much over 15 mm is unlikely to have a beneficial effect on these measures of flight performance as this species lacks any traits, such as longer wings, that have co-evolved with streamers.

In summary, the addition of small streamers to house martins has a range of effects on different aspects of flight performance: for variables determining maneuverability, outer tail feather length is optimized by a 6- to 10-mm increase. In contrast, for variables such as velocity and acceleration, outer tail feathers are probably at their optimum length and increasing their length appears to have a detrimental effect on flight performance. These results are consistent with the predictions made by

Thomas (1993) who stated that any extension of the tail beyond the maximum continuous span would increase drag and not lift. In addition, during straight flight when the tail is furred, the Norberg mechanism would not be able to operate and streamers are likely only to add to drag.

#### Evolutionary selection pressures on streamer development in hirundines

The results from this experiment suggest that hirundines may gain some aerodynamic benefit in terms of maneuverability through the evolution of streamers. This result is consistent with recent work testing the maneuverability of sand martins with manipulated tails (Rowe et al., in press). That two species of streamerless hirundine should react to tail manipulation in a similar way using entirely different methods of measuring flight performance indicates that this result is robust. Interestingly, Rowe et al. (in press) found that the optimal streamer length in sand martins exceeded the maximum 20-mm manipulation used in that experiment. Other than the fact that different species were investigated, the explanation for this apparent contradiction with our findings may lie in the different techniques used. Sand martins in that study were released into a flight maze which forces the birds to make very tight maneuvers around obstacles, whereas house martins in this study were free-flying. We were, therefore, investigating a different type of flight performance that may not be directly comparable. That streamer evolution has not occurred in many species of hirundine, including house martins and sand martins, suggests that there may be some selection pressure preventing streamer evolution. We suggest that this pressure may arise from the detrimental effect that initial streamer evolution has on aspects of flight performance relating to velocity and acceleration.

In summary, considerable evidence now shows that the addition of streamers to streamerless hirundines improves maneuverability in turning flight. This suggests that initial streamer evolution in ancestral barn swallows may have evolved through natural selection for maneuverability. We have shown quantitatively that barn swallows are more maneuverable than house martins during commuting flight (Fig. 3). The underlying mechanism behind the initial improvement in performance is, however, unclear. Norberg (1994) suggested that the evolution of tail streamers may have promoted increased maneuverability during turning flight. This mechanism relies on the aeroelastic properties of the streamer which presumably differ with changes in length. Whether this mechanism can operate at the short streamer lengths used in this experiment remains unknown. However, there is likely a monotone, increasing function describing the enhancement of lift and decrease of drag that would follow lengthening of a streamer of the outer tail feather (R.Å. Norberg, personal communication). Thomas (1993) postulated that in flight, a bird's tail

would bend, and that as pressure is not distributed evenly over the surface, the outer tail feathers would be subjected to a component of lateral pressure. As a result, the leading edges of the tail droop in a manner similar to that proposed for the Norberg mechanism (Thomas 1993). If this theory is correct, it is possible to envisage how streamers might operate under the Norberg mechanism even at small lengths.

The cost of sexually selected characters has been proposed to be partly offset by the co-evolution of other morphological, physiological or behavioral traits (Møller 1996). We have found evidence for an aerodynamic benefit of small tail streamers during turning flight. During straight flight, however, the streamer is likely to contribute only drag. Barn swallows have longer and larger wings than either house martins or sand martins, which have been interpreted as cost-reducing traits that have co-evolved alongside streamers (Møller 1996). The evolution of such traits appears to have increased the optimal length of the streamer, as barn swallows have optimal streamer lengths far in excess of those found for house martins in this study (Buchanan and Evans, 2000).

#### Tail morphology and flight performance in hirundines

By manipulating tail length and filming house martins in flight, we have been able to differentiate between different aspects of their flight performance. We have shown that, as predicted, flight variables differ in their response to increased outer tail feather length. Nesting behavior may also have influenced streamer evolution: barn swallows build open nests which allow their streamers to hang outside the nest, whereas house martins build closed nests, and sand martins nest in burrows. If this nesting behavior resulted in large asymmetries, from wear and tear on the streamer, maneuverability would be reduced to below that seen in the absence of streamers (Thomas 1993). Assuming house martin tail morphology is at an overall optimum, the advantage of increased maneuverability is apparently outweighed by the cost of streamers on other aspects of flight performance, and possibly on the species' ecology and life history. If environmental conditions altered such that the benefit of increased maneuverability surpassed the cost on other factors, we suggest that streamers may evolve in species currently without them.

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