Vane emargination of outer tail feathers improves flight manoeuvrability in streamerless hirundines, Hirundinidae

Piotr Matyjasiak[1,2*]**, Jolanta Matyjasiak**[1]**, Florentino de Lope**[3] **and Anders P. Møller**[2]

[1]*Centre for Ecological Research (formerly Institute of Ecology), Polish Academy of Sciences, PL-05-092 Łomianki, Poland*
[2]*Laboratoire de Parasitologie Evolutive, Université Pierre et Marie Curie, F-75252 Paris, France*
[3]*Departamento de Ciencias Morfológicas, Biología Celular y Animal, Facultad de Ciencias (Biológicas), Universidad de Extremadura, E-06071 Badajoz, Spain*

Recent studies have suggested that the proximal part of the swallow (*Hirundo rustica*) tail streamer appears to aid turning flight, as expected if streamers evolved initially purely through natural selection for enhanced manoeuvrability. However, the evolution of slender aerodynamically advantageous streamers is also predicted by an alternative hypothesis, which suggests that such a trait could develop primarily to ameliorate the aerodynamic cost of a long size-dimorphic tail. To distinguish between these hypotheses, we have investigated for the effect on manoeuvrability of trimming the tips of the outer tail feathers into short streamers, without lengthening these feathers, in two streamerless hirundine species—the house martin (*Delichon urbica*) and the sand martin (*Riparia riparia*). This allowed us to examine the aerodynamic costs and benefits of streamers at an early evolutionary stage that predates elongation of the outermost tail feathers through female choice. We showed that such initial streamers enhance manoeuvrability in streamerless hirundines, confirming the findings of recent studies. However, in contrast to these studies, we showed that improved manoeuvrability resulting from streamers could arise before the outermost tail feathers have become elongated (e.g. owing to female choice). The occurrence of such an aerodynamic advantage depends on the ancestral shape of a forked tail. This provides support for the hypothesis that streamers, like those in the barn swallow, might evolve initially purely through natural selection for enhanced manoeuvrability.

Keywords: bird flight; feather shape; Hirundinidae; natural selection; sexual selection; tail streamer

1. INTRODUCTION

Avian flight morphology is affected by a mixture of selection pressures and is thus an interesting example of how different selection forces initiate changes in morphological traits (Balmford *et al.* 1993, 1994; Møller *et al.* 1995). Elaborate male tail ornaments in some species are traditionally thought to have evolved through sexual selection (Darwin 1871; Andersson 1994). Tail morphology is also shaped by natural selection for aerodynamic performance (tails act as a control surface, contribute additional lift in turning or slow flight and reduce body drag), and aerodynamic calculations suggest that some forms of tail elongation may be favoured by natural, rather than sexual, selection (Balmford *et al.* 1993; Thomas 1993*a*; Thomas & Balmford 1995). Although elongation of graduated tails and pintails is agreed to develop purely through sexual selection (Evans & Thomas 1992; Balmford *et al.* 1993; Thomas 1993*a*), the relative role of natural and sexual selection in the evolution of forked tail ornaments is still discussed (Evans & Thomas 1997; Møller *et al.* 1998; Hedenström 2002).

A model species for studies of the function of avian tails is the barn swallow (*Hirundo rustica*) (Møller 1994). Male barn swallows have deeply forked tails with long

streamers—slender outermost tail feathers with equally narrow vanes on the two sides of the shaft at the tip of the feather; females have shorter streamers than males. Streamers appear to have evolved in the Hirundinidae independently at least three times from separate streamerless ancestors (Møller 1994) and are now present in many hirundine species (Turner & Rose 1989). Female barn swallows base their mate choice on male tail length (Møller 1988; Smith & Montgomerie 1991), although longer-tailed males contribute less to parental care than short-tailed males (Møller 1994). The length of male streamers appears to have a genetic basis and reflects inherent differences in phenotypic quality among males; however, long streamers impose a substantial viability cost upon males and are believed to evolve according to the handicap model of sexual signalling (Møller *et al.* 1998).

One supposed cause of cost of a long tail is aerodynamic drag. Theoretically, the amount of lift generated from a tail is determined by its maximum continuous span, while the drag is proportional to the total tail area (Thomas 1993*a*; but see Evans 2003). The aerodynamically optimal tail (producing maximum lift for a given drag) is triangular when spread and forked when furled. It follows, therefore, that evolutionary elongation of the outer tail feathers in forked tails is initially advantageous, but further elongation of these feathers into streamers will be costly as any surface protruding beyond the point of maximum continuous

1831

width adds drag but no lift. However, Norberg (1994) suggested an aeroelastic mechanism according to which streamers create a pitching moment about the outermost feather's long axis causing an automatic downward deflection of the tail's leading edge when the tail is spread and lowered. This may help to increase substantially tail-generated lift thus allowing tighter turns during foraging-manoeuvring flight (see also Thomas 1993*a*). Such an indirect aerodynamic function of swallow streamers, leading to enhanced manoeuvrability, puts into question sexual selection as the original selective force driving streamer evolution (Norberg 1994).

Current discussion about the origin of swallow streamers focuses on distinguishing between two alternatives. Evans & Thomas (1997) suggest that streamers could have evolved originally purely through natural selection for enhanced manoeuvrability. Buchanan & Evans (2000) and Rowe *et al.* (2001) have shown that the proximal part of the streamer appears to aid manoeuvrability, as measured in a flight maze or by stereo-video filming, and thus can be attributed to natural selection, whereas the distal part of the streamer is costly in terms of impaired manoeuvrability and thus can be viewed as sexually selected. Swallow streamers could have evolved initially via natural selection alone, and sexual selection might only later have increased their length beyond a naturally selected aerodynamic optimum (Buchanan & Evans 2000; Rowe *et al.* 2001).

By contrast, Møller *et al.* (1998) suggest that streamers evolved initially through elongation of the outermost tail feathers via sexual selection for costly signalling of quality, and only later have their vanes become narrow because of natural-selection costs. In a comparative study of avian tail morphology, Møller & Hedenström (1999) found that all bird species with long sexually size-dimorphic tails invariably develop narrower tail-feather tips with vanes of more equal width, as compared to closely related short-tailed size-monomorphic species, irrespective of tail shape and foraging mode. Vane asymmetry (the inner vane being wider than the outer vane), emargination and curvature of avian flight feathers are essential for an aerodynamic function of a feather as an aerofoil (Norberg 1990; Thomas 1993*a*), and loss of vane asymmetry is thought to indicate loss of aerodynamic function of a feather (Feduccia & Tordoff 1979). The evolution of slender feather tips with narrow vanes (including streamers) in species with long size-dimorphic tails is unlikely to be the product of female preference for a reduced width of tail feathers and has been attributed to a general mechanism for reducing the aerodynamic cost of a long tail ornament (Møller *et al.* 1995). (The drag of a feather is proportional to feather width; Thomas 1993*a*.) Sexual selection could initially have instigated the elongation of broad-tipped tail feathers, but natural selection concomitantly modified feather width leading to the development of a slender streamer. Consequently, it was not before streamers had become long and narrow owing to a cost-reducing modification of vane morphology that an indirect aerodynamic benefit of streamers arose (Møller *et al.* 1998; Møller & Hedenström 1999).

Recently Park *et al.* (2000) and Rowe *et al.* (2001) attempted to discriminate between these hypotheses by examining the effect of lengthening the tail with small artificial streamers on flight manoeuvrability of two
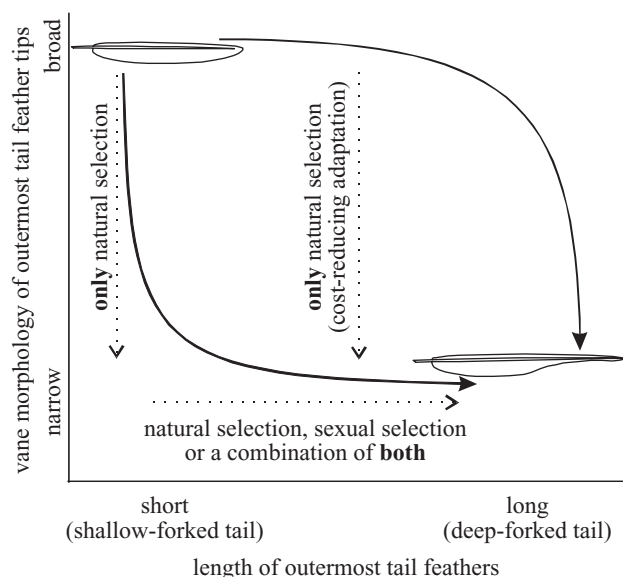

Figure 1. Morphology of the outermost-tail-feather vanes versus the length of these feathers during the evolution of tail streamers—a diagram of the experimental protocol employed in this study. This protocol separated the effects of streamer narrowing and streamer lengthening on manoeuvring flight and allowed us to examine the aerodynamic costs and benefits of streamers at an early evolutionary stage that predates their elongation through female choice. The outline of a feather at the upper-left corner of the diagram symbolizes an outermost tail feather with a broad and vane-asymmetric tip, present in streamerless size-monomorphic bird species. The outline of a feather at the lower-right corner of the diagram symbolizes an outermost tail feather with a long slender streamer, present in streamer-tailed birds.

streamerless hirundines that are closely related to the barn swallow. They showed that imitated streamers improved manoeuvrability in the manner predicted if streamers evolved initially according to the natural-selection hypothesis (Evans & Thomas 1997). The authors mimicked the early stage of streamer evolution by adding actual swallow streamers or narrow pieces of feathers resembling swallow streamers. However, these results could also be accommodated entirely by the alternative mechanism, in which narrow streamers are the product of modifications that reduce the flight cost of long sexually size-dimorphic tail feathers.

We suggest that, to distinguish between these hypotheses, it is necessary to distinguish between the effects of feather narrowing and those of feather lengthening on manoeuvrability and to examine the aerodynamic effect of small narrow streamers mimicking an early stage that predates the elongation of streamers through female choice (figure 1). In this study we achieved this with a standardized flight-maze experiment involving streamerless hirundines, in which we examined the effect on manoeuvrability of trimming the tips of the outermost tail feathers into short slender streamers, *without* lengthening these feathers. If improved manoeuvrability arose only after the outermost tail feathers became long and narrow (owing to sexual selection and a subsequent cost-reducing modification of feather vane width to form streamers; Møller & Hedenström 1999), we predict that experimental trimming of broad tips of the outermost tail feathers into slender

(a) 'natural-length' house martins

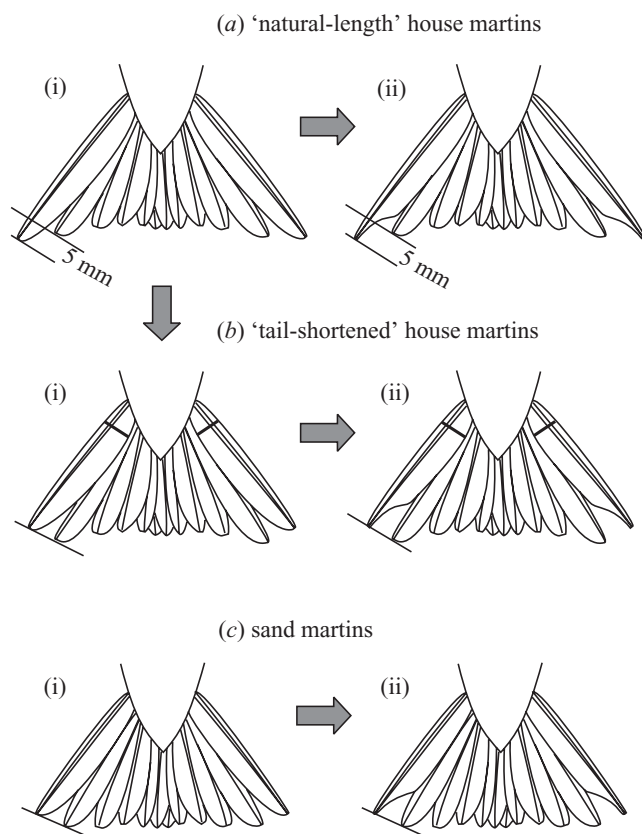(b) 'tail-shortened' house martins

(c) sand martins

Figure 2. Diagram of tail manipulations: trimming the tips of the outermost tail feathers into short slender streamers. (a) 'Natural-length' house martins: (i) 'broad-feather' and (ii) 'narrow-feather' birds. In house martins the outermost tail feathers are, on average, 5 mm longer than the second outer tail feathers. (b) 'Tail-shortened' house martins: (i) 'broad-feather' and (ii) 'narrow-feather' birds. The outermost tail feathers in this group were shortened by 5 mm to mimic the shallower-forked shape of a sand martin tail, in which the outermost and the second outer tail feathers are equal in length. (c) Sand martins: (i) 'broad-feather' and (ii) 'narrow-feather' birds.

streamers in streamerless tail-monomorphic species will not improve manoeuvrability.

We used house martins (*Delichon urbica*) and sand martins (*Riparia riparia*), streamerless size-monomorphic hirundines that were used previously by Park *et al.* (2000) and Rowe *et al.* (2001). The tail shape in these species resembles that in hypothetical ancestors of modern tail-ornamented swallows (Matyjasiak *et al.* 2000). In house martins, the outermost tail feather is, on average, 5 mm longer than the second outer tail feather, whereas in sand martins these feathers are of equal length; as a result house martins have slightly more forked tails than sand martins (figure 2). We used this interspecific difference to examine how initial tail morphology influences possible pathways of streamer evolution. To evaluate the manoeuvrability in a standardized manner we used a flight maze. A crowded maze environment presents birds with a standardized task that forces them to make increasingly tight turns around obstacles. The performance of individuals in a maze can be used as an assessment of manoeuvrability (Aldridge 1986; Møller 1991; Evans *et al.* 1994; Balmford *et al.* 2000; Rowe *et al.* 2001; Stockwell 2001).

2. MATERIAL AND METHODS

(a) *Species and study site*

Individual house martins and sand martins of both sexes were caught in the vicinity of Badajoz, Spain, using mist-nets in April and May 2002. This took place during the incubation phase of the breeding cycles of these species. House martins were caught at a colony (*ca.* 600 pairs) located in the University of Extremadura campus, Badajoz. Sand martins were caught at a colony (*ca.* 150 pairs) located in a gravel pit at the Guadiana River, Badajoz. We took the following biometric measurements: left and right flattened wing lengths, wingspan (the longest distance from one wing tip to the other, with the wing joints fully extended), left and right outermost tail feather lengths, and the length of the inner tail feather were measured to the nearest 1 mm with a ruler; head, bill, keel and left and right tarsus lengths were measured to the nearest 0.1 mm using a pair of callipers; body mass was measured to the nearest 0.1 g with a Pesola spring balance; and aspect ratio was calculated as $(\text{wingspan})^2/\text{wing area}$ (wing area was measured by making a tracing of the outlines of fully extended wings). The birds were sexed according to the presence and appearance of a brood patch (Svensson 1984).

(b) *Tail manipulations*

Individual house martins of both sexes were allocated randomly into four groups, and sand martins of both sexes were allocated randomly into two groups. Two house martin groups had the lengths of the outermost tail feathers left unchanged—hereafter named 'natural-length' house martins (figure 2a), and the remaining two house martin groups had the outermost tail feathers shortened by 5 mm—hereafter named 'tail-shortened' house martins (figure 2b)—to mimic the shallow-forked tail shape in the sand martin (figure 2c). Of the two 'natural-length' house martin groups, the two 'tail-shortened' house martin groups and the two sand martin groups (tail length left unchanged) one was the 'narrow-feather' group and the other was the 'broad-feather' group. 'Narrow-feather' groups had the distal parts of the outermost tail feathers trimmed into 5 mm long narrow streamer shapes (without lengthening these feathers), modelled on the streamers of the barn swallow (figure 2a(ii),b(ii),c(ii)). 'Broad-feather' groups received the same amount of handling, but no feathers were trimmed (figure 2a(i),b(i),c(i)). To assess the effect of trimming the tips of the outer tail feathers into short streamers on manoeuvrability, we paired 'narrow-feather' and 'broad-feather' birds within all three martin groups to perform paired comparisons of flight measures (see § 2c). 'Tail-shortened' house martins had 5 mm sections cut from the basal parts of their outer tail feathers, with cuts made under the tail coverts *ca.* 7 and 12 mm from the feather base. The proximal and distal parts of the feather were then re-attached and fixed using 5 mm micropins and a cyano-acrylic superglue (Smith & Montgomerie 1991; Park *et al.* 2000).

(c) *The flight maze*

We assessed manoeuvrability by releasing birds through a flight maze (18 m × 4 m × 1.6 m), adapted from Balmford *et al.* (2000) and Rowe *et al.* (2001). The maze consisted of a metal frame covered in a fine-mesh netting, with one end left open. Birds were released from a box at the closed end and flew through the maze to escape from the open end. The first 9 m section of the maze with the release box, was free of obstacles and acted as an acceleration zone. The remaining 9 m section towards the exit contained 16 successive panels of vertical strings suspended from the roof of the maze and acted as a test zone. Both the distance between the strings within a panel and the distances between

consecutive panels decreased towards the exit. The within-panel separation of the strings decreased from 70 cm at the beginning of the test zone (roughly twice the wingspan of a house martin) to 8 cm at the exit (roughly a quarter of the wingspan of a house martin). The between-panel distance decreased from 70 to 40 cm. The strings were placed so that each panel was offset from both the neighbouring panels. Each string was weighted to ensure that it hung vertically, but it could swing if hit. We measured the time taken for a bird to negotiate the maze test section and recorded the number of strings collided with en route, which were used as measures of the bird's ability to cope with the crowded maze environment. A faster flight time and/or fewer strings hit indicate greater manoeuvrability (Aldridge 1986; Evans *et al.* 1994; Balmford *et al.* 2000; Rowe *et al.* 2001). Dyads of 'narrow-feather'–'broad-feather' birds were released through the maze immediately after manipulation. The order of release within dyads was alternated.

(d) *Measurement of manoeuvrability*

The time taken to negotiate the stringed zone of the maze was measured based on video images (filming at 25 frames s^{-1}) obtained with the use of angled mirrors positioned in line with the first and last panels of strings. A bird's image was reflected in the first mirror as it entered the test section, and the second image was reflected in the other mirror when it left the maze. The flight time was taken as the number of successive video frames between the two images (accuracy of 0.04 s). One of us (J.M.), being unaware of the manipulation, recorded the number of string collisions by monitoring any movement of the strings from a shelter at the open end of the maze.

(e) *Statistical analysis*

The time taken to fly through the maze test section and the number of strings hit were not significantly correlated (see § 3), and we therefore conducted separate statistical analyses for these flight measures. First, we performed ANOVAs for each group of martins separately. Pairing of 'narrow-feather' and 'broad-feather' birds allowed comparisons of flight measures within dyads based on the morphology of the outermost tail-feather tips as a predictor variable. We therefore used ANOVA designs that included either flight time or number of strings hit as a dependent variable and one repeated-measures (within-subject) factor to compare within-dyad differences in flight measures. Second, we constructed complex general stepwise regression (GSR) models that included either flight time or number of strings hit as a dependent variable and groups of martins as independent categorical predictors. We calculated the difference between flight measures for each dyad (flight measure for the 'broad-feather' bird minus flight measure for the 'narrow-feather' bird), and this became a new dependent variable. We used date, sex and release order as categorical predictors, and within-dyad differences in morphological measures as continuous predictors (covariates). The initial model also included interactions between tail-manipulation factors and sex, date and morphological measurements. Insignificant variables were removed from the models, which were then rerun. However, those variables that significantly interacted with other variables in the model were not removed regardless of their significance. We checked residuals for a normal distribution and variances for homogeneity. The flight time, the number of strings hit and morphological variables were $\ln(x+1)$-transformed prior to analysis. We used STATISTICA 5.5A (Statsoft Inc. 1997).

Morphological variables are intercorrelated, and we therefore used principal components to construct new composite measures representing various aspects of the birds' morphology. 'Flight

apparatus' (FLAP) is the first principal component calculated from the five flight morphology variables: wing length, tail length, inner tail-feather length, wingspan and aspect ratio. 'Body size' (BOS) is the first principal component calculated from the three morphological variables: the lengths of the bill, tarsus and keel. Body mass was weakly correlated with the other morphological variables and thus was used as an individual variable. FLAP $= -0.35 \times$ wing $- 0.27 \times$ tail $- 0.21 \times$ innertail $- 0.36 \times$ wingspan $- 0.13 \times$ aspect ratio. This component explained 53% of the total variance, and the factor loadings were -0.92 for wing, -0.70 for tail, -0.55 for inner tail, -0.94 for wingspan and -0.34 for aspect ratio. BOS $= 0.46 \times$ bill $+ 0.45 \times$ tarsus $+ 0.44 \times$ keel. This component explained 55% of the total variance, and the factor loadings were 0.75 for bill, 0.74 for tarsus and 0.73 for keel.

3. RESULTS

Sixty-six birds were tested. We obtained the time taken to fly through the maze test section and the number of strings hit for 20 'natural-length' house martins (6 females and 14 males), 20 'tail-shortened' house martins (9 females and 11 males) and 26 sand martins (12 females and 14 males), and the numbers of dyads were 10, 10 and 13, respectively. The flight time was weakly positively, but not significantly, correlated with the number of strings hit ($r = 0.18$, $t_{66} = 1.44$, $p > 0.15$).

The effect of trimming the outer tail feathers into 5 mm narrow streamers on both flight measures was positive and significant in the 'natural-length' house martin group (figure 3*a*) (ANOVA, flight time: $F_{1,9} = 20.55$, $p < 0.005$; number of strings hit: $F_{1,9} = 6.02$, $p < 0.05$), but non-significant in the 'tail-shortened' house martin group (figure 3*b*) (ANOVA, flight time: $F_{1,9} = 0.01$, $p > 0.9$; number of strings hit: $F_{1,9} = 1.05$, $p > 0.3$) and in the sand martin group (figure 3*c*) (ANOVA, flight time: $F_{1,12} = 0.00$, $p > 0.95$; number of strings hit: $F_{1,12} = 0.03$, $p > 0.85$). The final GSR model explaining variation in the within-dyad differences in flight measures (flight measure for the 'broad-feather' bird minus flight measure for the 'narrow-feather' bird) among the martin groups after stepwise removal of the insignificant factors showed highly significant among-group variation in the effect of tail manipulation on both flight measures (table 1). The within-dyad differences in flight measures were significantly larger in the 'natural-length' house martin group than in the remaining martin groups (*a posteriori* Bonferroni test, which adjusts the significance levels for the individual *post hoc* comparisons; $p < 0.05$). Therefore, the data suggest that experimental narrowing of the tips of the outer tail feathers into short slender streamers resulted in improved manoeuvrability, but only in the house martin group with deeper-forked tails.

4. DISCUSSION

As measured by the flight-maze tests, trimming the outermost tail feathers into 5 mm long narrow streamers, without elongating these feathers, resulted in improved manoeuvrability in 'natural-length' house martins, but not in sand martins or in 'tail-shortened' house martins. 'Natural-length' house martins had tails with outermost tail feathers 5 mm longer than the second outer tail feathers, whereas the homologous feathers in sand martins and in 'tail-shortened' house martins were of equal length;
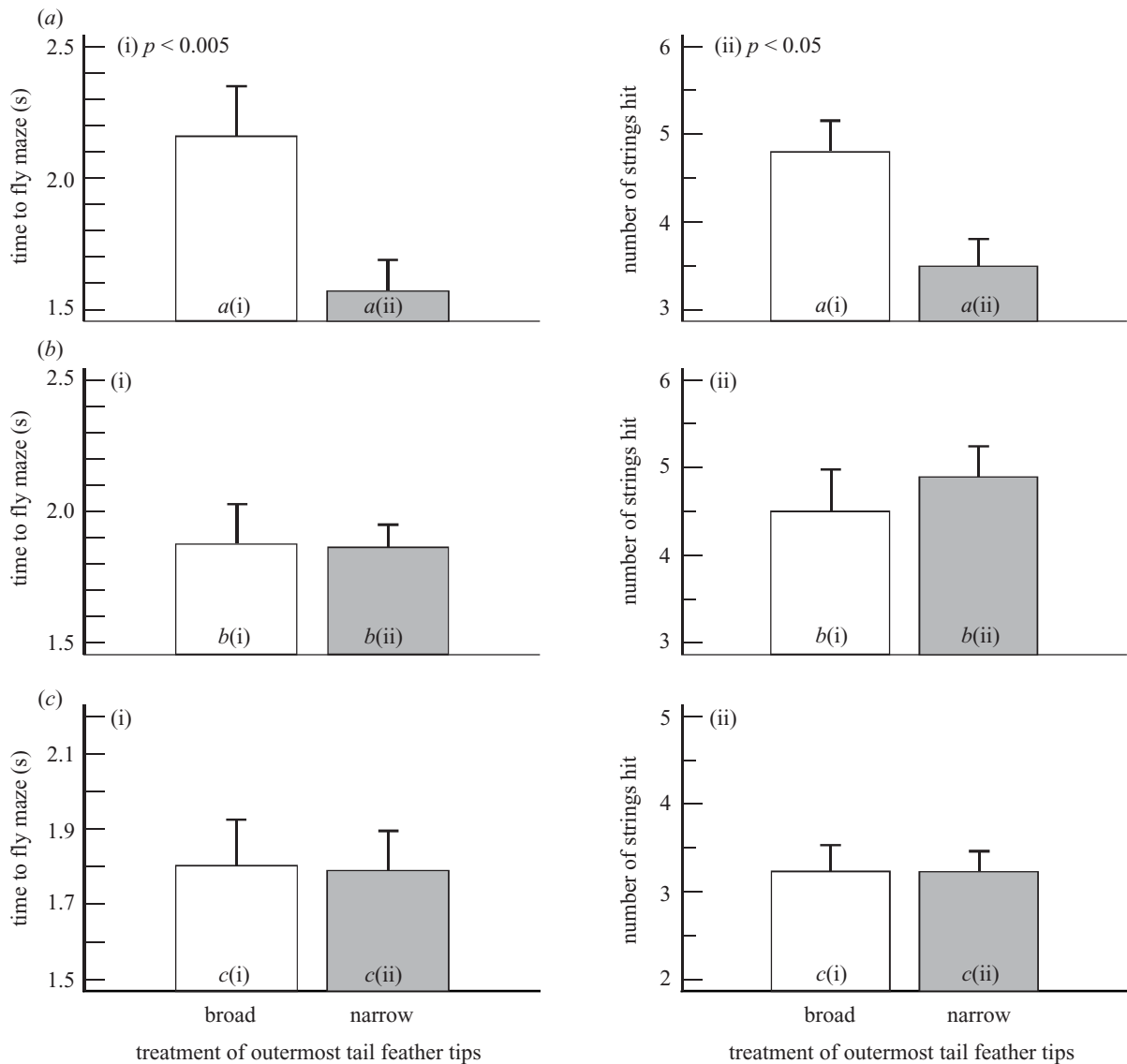
Figure 3. Effect of feather-tip manipulation on (i) flight time through the maze test section and (ii) the number of strings hit while doing so. (*a*) 'Natural-length' house martins; (*b*) 'tail-shortened' house martins; and (*c*) sand martins. The histograms show means + s.e. Labels on bars correspond to the tail-manipulation groups presented in figure 2.

Table 1. Results of complex GSR models testing the effects on flight performance measures of trimming the tips of the outer tail feathers into short slender streamers.
(FLAP: composite measure for 'flight apparatus'.)

	flight time				number of strings hit		
	F	d.f.	p		F	d.f.	p
group	6.13	2,26	< 0.01		8.15	2,25	< 0.005
release order	—	—	—		6.40	1,25	< 0.05
sex	2.95	3,26	< 0.05		—	—	—
FLAP	—	—	—		11.88	1,25	< 0.005
group × FLAP	—	—	—		9.62	2,25	< 0.001
overall model	$r^2 = 0.33$ 4.06	5,26	< 0.01	$r^2 = 0.56$	7.57	6,25	< 0.001

—, not significant.

in the latter group, the tail shape was modified experimentally to mimic tail morphology in the sand martin (figure 2). Therefore, we show that, in accordance with the results of theoretical (Evans & Thomas 1997) and empirical (Park *et al.* 2000; Rowe *et al.* 2001) studies, narrow streamers can

enhance manoeuvrability in streamerless hirundines. However, contrary to previous studies, we show that improved manoeuvrability resulting from streamers can arise *before* the outermost tail feathers have become elongated (e.g. owing to sexual selection). It follows that, compatible with

the improved-manoeuvrability hypothesis (Norberg 1994; Evans & Thomas 1997), streamers similar to those in the barn swallow could evolve in streamerless species initially purely through natural selection for enhanced manoeuvrability.

The occurrence of this aerodynamic advantage depends on the ancestral shape and depth of the forked tail and, in particular, on the relative length of the first and second outer tail feathers. If the outermost tail feathers are initially longer than the second outer tail feathers, as in extant house martins, then prior tail elongation under sexual selection, or selective pressure other than selection for enhanced manoeuvrability, is not necessary for the development of aerodynamically functional streamers. This reduces the general significance of the mechanism proposed by Møller & Hedenström (1999), limiting it to very shallow forked tails resembling that in the sand martin (and also to graduated tails and pintails). In the case of very shallow forked tails this mechanism may govern the evolution of slender streamers subsequent to a costly stage of elongation of tail feathers into broad streamers through sexual selection. This idea finds support in another experiment (P. Matyjasiak, F. de Lope and A. P. Møller, unpublished data), in which we mimicked the early streamer elongation by contrasting the effects of adding a broad piece of feather and a narrow piece of feather on manoeuvrability, showing that narrowing the experimentally elongated streamers results in improved manoeuvrability. By contrast, selection for increased manoeuvrability acting on a species with a very shallow-forked tail might lead to the evolution of slender streamers by concurrent evolutionary lengthening and narrowing of the tips of the outermost tail feathers (e.g. an evolutionary transition from the 'tail-shortened' house-martin-like stage to the 'natural-length' house-martin-like stage). The above scenarios assume that forked tails have developed in sand martins and house martins by evolutionary elongation of the outermost tail feathers from a simple ancestral tail with all feathers of equal length. An inspection of the phylogeny of Hirundinidae (Sheldon & Winkler 1993) suggests that this is very probably the case for the sand martin. In the case of the house martin, however, it is equally likely that the extant tail shape might have developed through evolutionary shortening of the outermost tail feathers in a deeply forked sexually size-dimorphic tail in the hypothetical house martin ancestor, after selection for a long tail had ceased.

House martins and sand martins have not evolved long streamers presumably because such streamers, while aiding manoeuvrability, are detrimental to flight measures that are directly related to velocity and acceleration, which may be more important for foraging success than the ability to make tight turns (Park *et al.* 2000). Matyjasiak *et al.* (1999, 2000) have shown that experimentally elongated outermost tail feathers impair foraging success in the sand martin and have discussed mechanisms that could potentially explain the initial evolution of size-dimorphic streamers according to the handicap principle. Such a cost could inhibit the evolution of streamers through tail-feather elongation in the sand martin, but it is unlikely to inhibit the development of streamers by evolutionary narrowing of the outermost tail-feather tips without preceding tail elongation in the house martin. In the latter case, initial streamers would not increase the total tail area, and, in accordance

with theory (Thomas 1993*a*), they would not increase the aerodynamic drag generated from the tail. The enhanced manoeuvrability offered by short narrow streamers could aid house martins during their pursuit of strong flying insects, also enabling them to avoid collisions with large insects in the air or with other martins in crowded breeding colonies. Like barn swallows, house martins hunt for insects on the wing, but unlike barn swallows they select small insects (Bryant & Turner 1982; Turner 1982). Small insects may be less demanding in terms of manoeuvrability for a bird pursuing them in the air. In fact, Park *et al.* (2000) have shown that manoeuvring is of less importance in commuting flight in house martins than in barn swallows. During forward flight the tail is furled and streamers cannot generate substantial aerodynamic forces. Therefore, greater manoeuvrability resulting from possessing short narrow streamers may not directly translate into enhanced hunting success in house martins and thus may be useless for this species, although this point should be verified experimentally. House martins and sand martins have already developed tails of a forked shape, which is presumably aerodynamically optimal and which might have been exaggerated from a simple tail through natural selection for optimizing the lift–drag ratio (Balmford *et al.* 1993; Thomas 1993*a*). In such a forked tail, broad-tipped outermost tail feathers could droop sufficiently to form a leading-edge suction in a manner resembling the Norberg mechanism (Thomas 1993*a*).

The evolution of long narrow streamers in house martins and sand martins may also be constrained by nesting habits. Unlike barn swallows, these hirundines nest in enclosed spaces. This may result in more wear and breakage of longer streamers than of short ones and—in our experiment, in which tail feathers were not elongated—more damage to narrow feather tips than to broad feather tips. A broken feather tip results in tail asymmetry, which increases the flight cost and reduces manoeuvrability (Møller 1991; Thomas 1993*b*; Evans *et al.* 1994). However, we have found no cases of feather-tip breakage in narrow-feather or broad-feather birds (P. Matyjasiak, F. de Lope and A. P. Møller, unpublished data).

Turning performance is directly determined by the amount of lift a tail produces and is also proportional to tail area and thus to the amount of tail-generated drag (Thomas 1993*a*, 1996). The lengths of the outermost tail feathers in 'natural-length' house martins were not manipulated. Therefore, we did not change the maximum continuous span or the total area of the tails. Nevertheless, in this martin group 'narrow-feather' birds manoeuvred better than 'broad-feather' birds. It is plausible that initial streamers improved manoeuvrability in 'narrow-feather' birds through a mechanism suggested by Norberg (1994). In our experiment we did not affect the integrity of the outermost tail feathers, except for trimming the 5 mm long distal part. Presumably, experimentally narrowed feather tips bent to align with the air-stream to a larger extent than naturally broad feather tips, causing a greater pitching moment about the outermost feather's torsion axis and creating a more deflected leading edge of the tail. This effect probably cannot be attained when the outermost and the second outer tail feathers are the same length, as in sand martins and 'tail-shortened' house martins. In this case the tail feathers may be too short for imitated streamers to

cause a significant twisting force about the outermost tail feather's torsion axis. It seems, therefore, that the Norberg (1994) mechanism may operate even with very short initial streamers provided that the outermost tail feather is longer than the second outer tail feather, as it is in the case of house martins.

In conclusion, our results suggest that, owing to the aerodynamic advantage of narrowed tips of the outermost tail feathers (dependent on the relative length of the first and second outer tail feathers), the evolution of narrow streamers may predate the association of female preference with the length of the outermost tail feathers. It follows therefore that, contrary to the proposition by Møller *et al.* (1998) and Møller & Hedenström (1999), sexual selection is not the only possible explanation for the origin of swallow streamers.

REFERENCES

Aldridge, H. D. N. J. 1986 Manoeuvrability and ecological separation in the little brown (*Myotis lucifugus*) and Yuma (*M. yumanensis*) bats (Chiroptera: Vespertilionidae). *Can. J. Zool.* **64**, 1878–1882.

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Balmford, A., Thomas, A. L. R. & Jones, I. L. 1993 Aerodynamics and the evolution of long tails in birds. *Nature* **361**, 628–631.

Balmford, A., Jones, I. L. & Thomas, A. L. R. 1994 How to compensate for costly sexually selected tails: the origin of sexually dimorphic wings in long-tailed birds. *Evolution* **48**, 1062–1070.

Balmford, A., Lewis, M. J., Brooke, M. de L., Thomas, A. L. R. & Johnson, C. N. 2000 Experimental analyses of sexual and natural selection on short tails in a polygynous warbler. *Proc. R. Soc. Lond.* B **267**, 1121–1128. (DOI 10.1098/rspb.2000.1117.)

Bryant, D. M. & Turner, A. K. 1982 Central place foraging by swallows (Hirundinidae): the question of load size. *Anim. Behav.* **30**, 845–856.

Buchanan, K. L. & Evans, M. R. 2000 The effect of tail streamer length on aerodynamic performance in the barn swallow. *Behav. Ecol.* **11**, 228–238.

Darwin, C. 1871 *Descent of man, and selection in relation to sex*, 1st edn. (reprinted 1981). Princeton University Press.

Evans, M. R. 2003 Birds' tails do act like delta wings but delta-wing theory does not always predict the forces they generate. *Proc. R. Soc. Lond.* B **270**, 1379–1385. (DOI 10.1098/rspb.2003.2373.)

Evans, M. R. & Thomas, A. L. R. 1992 The aerodynamic and mechanical effects of elongated tails in the scarlet-tufted malachite sunbird: measuring the cost of a handicap. *Anim. Behav.* **43**, 337–347.

Evans, M. R. & Thomas, A. L. R. 1997 Testing the functional significance of tail streamers. *Proc. R. Soc. Lond.* B **264**, 211–217. (DOI 10.1098/rspb.1997.0030.)

Evans, M. R., Martins, T. L. F. & Haley, M. 1994 The asymmetrical cost of tail elongation in red-billed streamertails. *Proc. R. Soc. Lond.* B **256**, 97–103.

Feduccia, A. & Tordoff, H. B. 1979 Feathers of *Archaeopteryx*: asymmetric vanes indicate aerodynamic function. *Science* **203**, 1021–1022.

Hedenström, A. 2002 Aerodynamics, evolution and ecology of avian flight. *Trends Ecol. Evol.* **17**, 415–422.

Matyjasiak, P., Jabłoński, P. G., Olejniczak, I., Boniecki, P. & Lee, S.-D. 1999 Foraging cost of a long tail ornament: an experiment with sand martin females. *Ethology* **105**, 521–530.

Matyjasiak, P., Jabłoński, P. G., Olejniczak, I. & Boniecki, P. 2000 Imitating the initial evolutionary stage of a tail ornament. *Evolution* **54**, 704–711.

Møller, A. P. 1988 Female choice selects for male sexual tail ornament in the monogamous swallow. *Nature* **332**, 640–642.

Møller, A. P. 1991 Sexual ornament size and the cost of fluctuating asymmetry. *Proc. R. Soc. Lond.* B **243**, 59–62.

Møller, A. P. 1994 *Sexual selection and the barn swallow*. Oxford University Press.

Møller, A. P. & Hedenström, A. 1999 Comparative evidence for costs of secondary sexual characters: adaptive vane emargination of ornamented feather in birds. *J. Evol. Biol.* **12**, 296–305.

Møller, A. P., de Lope, F. & Saino, N. 1995 Sexual selection in the barn swallow *Hirundo rustica*. VI. Aerodynamic adaptations. *J. Evol. Biol.* **8**, 671–687.

Møller, A. P., Barbosa, A., Cuervo, J. J., de Lope, F., Merino, S. & Saino, N. 1998 Sexual selection and tail streamers in the barn swallow. *Proc. R. Soc. Lond.* B **265**, 409–414. (DOI 10.1098/rspb.1998.0309.)

Norberg, R. Å. 1994 Swallow tail streamer is a mechanical device for self-deflection of tail leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proc. R. Soc. Lond.* B **257**, 227–233.

Norberg, U. M. 1990 *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. Berlin: Springer.

Park, K. J., Evans, M. R. & Buchanan, K. L. 2000 Flight performance in house martins (*Delichon urbica*): the aerodynamic role of tail streamers in hirundines. *Behav. Ecol. Sociobiol.* **48**, 364–372.

Rowe, L. V., Evans, M. R. & Buchanan, K. L. 2001 The function and evolution of the tail streamer in hirundines. *Behav. Ecol.* **12**, 157–163.

Sheldon, F. H. & Winkler, D. W. 1993 Intergeneric phylogenetic relationships of swallows estimated by DNA–DNA hybridization. *Auk* **110**, 798–824.

Smith, H. G. & Montgomerie, R. 1991 Sexual selection and the tail ornaments of North American barn swallows. *Behav. Ecol. Sociobiol.* **28**, 195–201.

Statsoft Inc. 1997 *Statistica for Windows (Computer program manual)*. Tulsa: Statsoft Inc.

Stockwell, E. F. 2001 Morphology and flight manoeuvrability in the New World leaf-nosed bats (Chiroptera: Phyllostomatidae). *J. Zool. Lond.* **254**, 505–514.

Svensson, L. 1984 *Identification guide to European passerines*. Stockholm: The British Trust for Ornithology.

Thomas, A. L. R. 1993a On the aerodynamics of birds' tails. *Phil. Trans. R. Soc. Lond.* B **340**, 361–380.

Thomas, A. L. R. 1993b The aerodynamic costs of asymmetry in the wings and tail in birds: asymmetric birds can't fly round tight corners. *Proc. R. Soc. Lond.* B **254**, 181–189.

Thomas, A. L. R. 1996 The flight of birds that have wings and tail: variable geometry expands the envelope of flight performance. *J. Theor. Biol.* **183**, 237–245.

Thomas, A. L. R. & Balmford, A. 1995 How natural selection shapes bird's tails. *Am. Nat.* **146**, 848–868.

Turner, A. K. 1982 Optimal foraging by the swallow: prey size selection. *Anim. Behav.* **30**, 862–872.

Turner, A. K. & Rose, C. 1989 *Swallows and martins of the world*. London: Christopher Helm.