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Fine morphology of experimental tail streamers and flight manoeuvrability in the house martin *Delichon urbica*

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Summary

1. Recent studies suggest that long tail streamers (narrow outermost tail feathers) of the barn swallow *Hirundo rustica*, Linnaeus have initially evolved purely via natural selection for enhanced manoeuvrability. According to an alternative view, streamers have evolved initially solely via sexual selection for costly signalling, and their slender profile is merely an adaptation reducing the aerodynamic cost of a long tail ornament.

2. In order to distinguish between these alternative hypotheses we performed a standardized flight-maze experiment, in which we imitated the initial elongation of outermost tail feathers in a streamer-less hirundine, the house martin *Delichon urbica*, Linnaeus, contrasting the effects on flight manoeuvrability from adding either a broad or a narrow piece of feather.

3. 'Narrow-feathered' house martins (which had initial tail streamers modelled on a natural streamer of the barn swallow) manoeuvred better than 'broad-feathered' house martins (which had the natural shape of tips of experimentally elongated outermost tail feathers left unchanged), independent of elongation of the feather.

4. A small elongation of outermost tail feathers did not significantly improve manoeuvrability either in the case of 'narrow-feathered' or 'broad-feathered' birds.

5. These results suggest that it is the slender shape, but not elongation of streamers that is important for manoeuvrability, and thus streamer elongation is better explained by the sexual-selection than the improved-manoeuvrability hypothesis. We discuss hypothetical scenarios for evolution of hirundine tail streamers.

Key-words: feather shape, flight performance, natural selection, sexual selection, tail elongation

Introduction

Birds' tails are influenced by a variety of interacting selection pressures and thus are a good model system for studies of how different evolutionary forces initiate changes in morphology (e.g. Balmford *et al.* 1993; Thomas & Balmford 1995; Hedenström 2002; Evans 2004). However, in some instances different selection pressures might have the same effect on tail morphology, at least for a certain period of time, making it difficult to resolve which one is actually the cause of the evolutionary change. Such a case is the evolution of the long sexually size-dimorphic tails with streamers (elongated outermost tail feathers) in the barn swallow (*Hirundo rustica*, Linnaeus) (Evans & Thomas 1997; Møller *et al.* 1998; Matyjasiak & Jabłoński 2001; Møller & Barbosa 2001; Park *et al.* 2001).

Two hypotheses have been put forward to explain the evolution of barn swallow tail streamers. According to the sexual-selection hypothesis (Møller *et al.* 1998), streamers may have evolved initially solely via sexual selection as a costly signal of quality, in accordance with the handicap principle. barn swallow females have shorter streamers than males (Bańbura 1986; Møller 1994). Females base their mate choice on male tail length (Møller 1988; Smith & Montgomerie 1991), although longer tailed males contribute less to

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*Correspondence author. E-mail: piotr_matyjasiak@poczta.onet.pl 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, elongated outermost tail feathers are costly to males, and the costs include aerodynamic cost (Thomas 1993; Barbosa & Møller 1999), impaired foraging and viability (Møller & de Lope 1994; Møller *et al.* 1995a) and increased risk of predation, parasitism and disease (Saino & Møller 1996; Møller & Nielsen 1997; Saino, Bolzern & Møller 1997). Slender shape of streamers was suggested to be an adaptation of their fine morphology reducing the aerodynamic cost of tail ornaments, and to indicate loss of a function of these feathers in the context of selection for flight performance (Møller *et al.* 1995b, 1998; Møller & Hedenström 1999).

By contrast, the improved-manoeuvrability hypothesis (Evans & Thomas 1997) suggests that barn swallow streamers might have an indirect aerodynamic function in the context of selection for improved manoeuvrability. Norberg (1994) proposed that the primary function of streamers is to improve the aerodynamic performance of the basal part of these feathers during slow or turning flight. He proposed an aero-elastic mechanism, according to which streamers create a pitching moment about the outermost tail feather's long axis causing an automatic downward deflection of the tail's leading edge when the tail is spread and lowered. This may considerably increase tail-generated lift thus allowing for tighter turns (Thomas 1993; Evans & Thomas 1997). Several studies have reported a curvilinear relationship between length of Swallow streamers and manoeuvrability as measured in a flight maze or by stereo-video filming (Evans 1998; Buchanan & Evans 2000; Rowe *et al.* 2001; Bro-Jørgensen *et al.* 2007). These studies suggested that the proximal part of the streamer aids manoeuvrability and hence could 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.

Park *et al.* (2000) attempted to discriminate between these hypotheses by investigating the effects of lengthening the tail with small, imitated streamers on manoeuvrability of streamer-less hirundines. They confirmed the aerodynamic theory that a small elongation of outermost tail feathers augments turning flight and suggested that initial evolution of streamers was via selection for manoeuvrability at a cost to flight velocity and acceleration. Matyjasiak *et al.* (2004) noted that elongated outermost tail feathers are both long and narrow (Fig. 1), and the narrowness of these feathers may actually be the reason behind improved manoeuvrability (perhaps in combination with elongation). Park *et al.* (2000) imitated the early stage of swallow streamer elongation by adding actual streamers, which are narrow, so their experiment did not distinguish between these hypotheses. Distinction between the effects of feather narrowing and those of feather lengthening on manoeuvrability is important, because if it is the narrowness and not elongation of streamers that is important in turning flight then streamer elongation is better explained by the sexual-selection hypothesis.

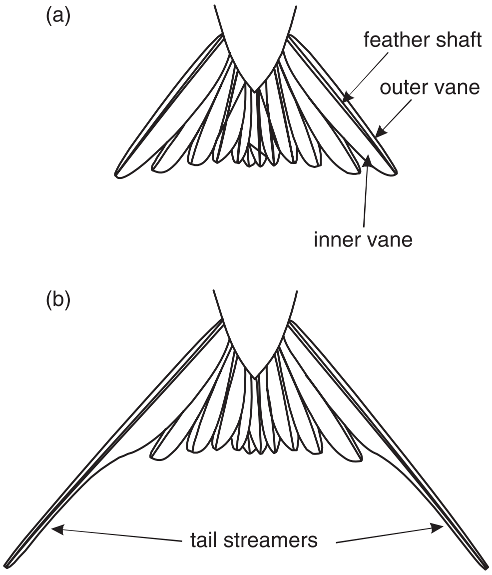

Fig. 1. Morphological components of the outermost tail feathers in (a) sexually size-monomorphic streamer-less hirundines and (b) sexually size-dimorphic hirundines with streamers. Note that streamers are not merely elongated versions of sexually size-monomorphic outermost tail feathers of streamer-less hirundines, but are slender with similarly narrow vanes on the two sides of the shaft at the apical part of the feather. Outermost tail feathers in streamer-less species have broad tips with asymmetric vanes (the outer vane is narrower than the inner vane).

Matyjasiak *et al.* (2004) tested the improved-manoeuvrability hypothesis and confirmed that short narrow streamers improved manoeuvrability. Their experiment could not support either the sexual-selection model or the improved-manoeuvrability model of streamer evolution, however, because they did not test for the effects on manoeuvrability of combined feather narrowing and feather lengthening.

In this study we distinguish between the effects of feather lengthening and those of feather narrowing on flight manoeuvrability in a fully factorial design. We performed a standardized flight-maze experiment, in which we imitated the early elongation of outermost tail feathers into streamers contrasting the effect on manoeuvrability from adding a broad piece of feather and a narrow piece of feather. We used house martins *Delichon urbica*, Linnaeus, a streamer-less size-monomorphic hirundine that was studied previously by Park *et al.* (2000) and Matyjasiak *et al.* (2004). The house martin is closely related to the barn swallow and the tail shape of this species resembles that of hypothetical ancestors of modern tail-ornamented hirundines (Matyjasiak *et al.* 2000). We evaluated manoeuvrability in a standardised manner using a flight maze. A crowded maze environment presents birds with a standardised task that forces them to make increasingly tight turns around obstacles. The performance of individuals in a maze can be used for an assessment of manoeuvrability (Aldridge 1986; Møller 1991; Evans *et al.* 1994; Balmford *et al.* 2000; Rowe *et al.* 2001; Bro-Jørgensen *et al.* 2007).

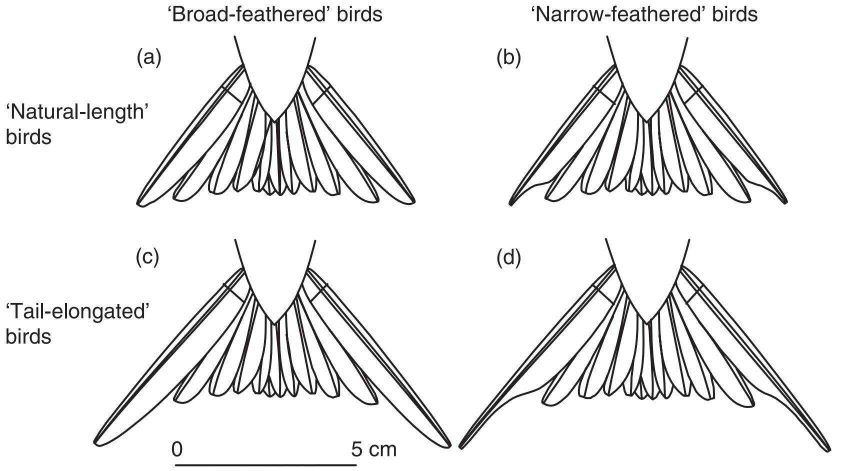

Fig. 2. Diagrams of tail manipulations applied to imitate the elongation of outermost tail feathers in house martins. 'Natural-length' manipulation groups: (a) 'broad-feathered' group, in which the outermost tail feather tips were left naturally broad with the inner vane being wider than the outer vane; and (b) 'narrow-feathered' group, in which the tips of outermost tail feathers were trimmed into narrow 'streamer' shapes with equally narrow vanes. 'Tail-elongated' manipulation groups: experimental 5, 10 and 15 mm tail elongation groups for (c) broad outermost feather tips and (d) narrow outermost feather tips.

Material and methods

FIELD METHODS

The study was conducted in 2002 in a large (*c*. 600 pairs) house martin colony located in the RUCAB, University of Extremadura, Badajoz, South-western Spain (38°50′ N, 6°59′ E). House martins of both sexes were captured with the use of mist nets during the incubation phase of the first brood of this species (second and third weeks of April). We took the following biometric measurements: left and right flattened wing length, 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 feathers 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 0·5 g with a Pesola spring balance; and aspect ratio was calculated as (wing span)^2/wing area (wing area was measured by making a tracing of the outlines of fully extended wings). The birds were sexed according to presence and appearance of a brood patch (Svensson 1984).

TAIL MANIPULATIONS

Individual house martins of both sexes were randomly assigned to 10 groups. Five groups, hereafter named 'broad-feathered' or B groups, had the natural shape of the outermost tail feather tips left unchanged (feather tips in B birds were broad with the outer vane narrower than the inner vane; Fig. 2a,c). Three of these five B groups were 'tail-elongated' groups (B5, B10 and B15) and two were 'natural-length' groups (B0a and B0b). 'Tail-elongated' B5, B10 and B15 birds had the two outermost tail feathers cut and replaced with outermost tail feathers, taken from a house martin, that were longer than the original feather. The post-manipulation length of outermost tail feathers in B5, B10 and B15 groups was increased by 5, 10 or 15 mm, respectively. The 'natural-length' B0a group had the outer tail feathers cut and re-glued without changing feather length (to control for the effect of feather cutting and gluing). 'Natural-length' B0b birds obtained the same amount of handling, but no feathers were cut. The remaining five groups (hereafter named 'narrow-feathered' or N groups) had the tips of the outermost tail feathers trimmed into narrow 'streamer' shapes with equally narrow vanes modelled on natural streamers of the barn swallow (Fig. 2b,d). Three of these five N groups were 'tail-elongated' groups (N5, N10 and N15) and two were 'natural-length' groups (N0a and N0b). 'Tail-elongated' N5, N10 and N15 birds had the two outermost tail feathers cut and replaced with outermost tail feathers, taken from a House Martin, that were longer than the original feather. The post-manipulation length of outermost tail feathers in N5, N10 and N15 groups was increased by 5, 10 or 15 mm, respectively. 'Natural-length' N0a group had the outer tail feathers cut and re-glued without changing feather length. 'Natural-length' N0b birds obtained the same amount of handling, but no feathers were cut. Feathers were cut under the tail coverts *c*. 7–12 mm from the feather base. The proximal and distal parts of the feathers were attached and fixed using 5 mm micropins and a cyano-acrylic super-glue (Smith & Montgomerie 1991; Park *et al*. 2000).

THE FLIGHT MAZE AND MEASUREMENTS OF MANOEUVRABILITY

We assessed manoeuvrability by releasing birds through a flight maze measuring 18 × 4 × 1·6 m, adapted from Rowe *et al*. (2001). The maze consisted of a metal frame covered in a fine-mesh netting, with its long axis being oriented west-east. The west end of the maze was closed and the east end was 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 (e.g. Balmford *et al*. 2000; Rowe *et al*. 2001; Bro-Jørgensen *et al*. 2007). The time birds are kept waiting for trials may affect their flight performance in the maze (P. Matyjasiak, unpublished data). For this reason we paired B0a and N0a, B0b and N0b, B5 and N5, B10 and N10, and B15 and N15 birds, so that comparisons of flight performance (see below) between 'broad-feathered' birds and 'narrow-feathered' birds were paired, unless otherwise stated. Dyads of B-N birds were released through the maze immediately after manipulation. The order of release within dyads was alternated.

Time taken to negotiate the maze stringed section 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 estimated as the number of successive video frames between the two images (accuracy of 0·04 s). An independent observer, being unaware of the manipulation, recorded the number of string clashes by monitoring any movement of the strings from a shelter at the open end of the maze.

STATISTICAL ANALYSIS

The time taken to fly through the maze test section and the number of strings hit were not significantly correlated (see Results), and we therefore conducted separate statistical analyses for these flight measures. First, we constructed simple general linear ANOVA models that included either flight time or number of strings hit as a dependent variable, and tail elongation factor and within-dyad release order as categorical predictors. This allowed us to determine which manipulation group means differed significantly. Then we re-ran the models including tail elongation factor as a continuous predictor (both linear and quadratic terms), with the intention of determining if there was a continuous effect of tail lengthening, and whether this effect was linear or curved. Pairing of B and N birds allowed comparisons of flight performance 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, tail elongation as a continuous predictor, date, sex and release order as categorical predictors, and morphological measurements and estimates of wing and tail fluctuating asymmetry (an absolute difference between the left and right wing or tail lengths, respectively) as continuous predictors. GSR does not allow for repeated measures design, and hence the streamer morphology was included as a between-group factor and within-day release order, instead of within-dyad release order, was used as a continuous covariate. Initial models also included interactions between 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. Flight time, 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 inter-correlated, and we therefore used principal components to construct new composite variables 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 = –0·37 × wing – 0·31 × tail – 0·21 × inner tail – 0·35 × wingspan–0·01 × aspect ratio. This component explained 49% of the total variance, and the factor loadings were –0·91 for wing, –0·78 for tail, –0·53 for inner tail, –0·87 for wingspan, and –0·02 for aspect ratio. BOS = 0·37 × bill + 0·52 × tarsus + 0·51 × keel. This component explained 50% of the total variance, and the factor loadings were 0·54 for bill, 0·78 for tarsus and 0·77 for keel. The two composite variables and body mass were weakly positively correlated (Pearson's correlation coefficients, FLAP and BOS $r = 0·37$, FLAP body mass $r = 0·15$, BOS and body mass $r = 0·29$).

Results

We obtained the time taken to fly through the maze test section and the number of strings hit en route for 100 House Martins (62 males and 38 females). Flight time was weakly, but not significantly positively correlated with number of strings hit ($r = 0·09$, $t_{100} = 0·87$, $P > 0·3$). Cutting and gluing of tail feathers did not have a significant effect on House Martin flight performance measures (flight time $F_{1,37} = 0·84$, $P > 0·35$; no. strings hit $F_{1,37} = 0·00$, $P > 0·98$), and hence we pooled B0a and B0b groups into one B0 group and N0a and N0b groups into one N0 group.

The simple general linear ANOVA models including either flight time or number of strings hit as a dependent variable, streamer width as a repeated measures factor, and tail elongation and within-dyad release order as categorical predictors had a significant effect of streamer width (flight time $F_{1,42} = 4·17$, $P < 0·05$; no. strings hit $F_{1,42} = 12·99$, $P < 0·001$). Flight time through the stringed section was significantly faster and number of strings hit en route was significantly lower in the case of 'narrow-feathered' than 'broad-feathered' birds. Of the two flight variables only number of strings hit was significantly predicted by a categorical elongation factor (flight time $F_{3,42} = 0·62$, $P > 0·6$; no. strings hit $F_{3,42} = 3·23$, $P < 0·05$). However, there were no significant differences between elongation group means (Bonferroni *post-hoc* test for multiple comparisons). Streamer width also predicted both flight variables in simple ANOVA models that included tail elongation as a continuous predictor (Table 1, Fig. 3). The effect of tail elongation on flight performance was significant (both linear and quadratic elongation terms) only in the case of number of strings hit (Table 1, Fig. 3). The linear relationship between number of strings hit while flying through the maze and elongation was negative and the curvilinear relationship was *u*-shaped. In the simple model for flight time, the quadratic elongation term did not explain a significant amount of variation in the flight measure and was removed in order to assess the importance of the linear elongation term to the model.

The final GSR model explaining individual variation in flight time had a significant effect of streamer width. Effects of tail elongation (both linear and quadratic elongation terms) were not significant (the quadratic elongation term was not retained in the model; overall model $r^2 = 0·07$; $F_{6,93} = 2·15$, $P < 0·05$; Table 1). Effects of both linear and

Table 1. Simple and complex general linear models showing the effect of elongating the outermost tail feathers of house martins with broad pieces of feather and narrow pieces of feather on measures of manoeuvrability

	Results from the simple GLM ANOVA models		Final results from the complex GSR models	
Source of variation	Flight time	No. strings hit	Flight time (slope, 1 SE)	No. strings hit (slope, 1 SE)
Streamer width	$F_{1,46}$ = 5·88*	$F_{1,44}$ = 8·09**	$F_{1,93}$ = 5·24* (0·0772, 0·033)	$F_{1,89}$ = 9·00** (0·0046, 0·001)
Elongation	$F_{1,46}$ = 1·32	$F_{1,44}$ = 6·45*	$F_{1,93}$ = 1·30	$F_{1,89}$ = 4·57* (–0·0015, 0·0007)
Elongation^2	–	$F_{1,44}$ = 5·17*		$F_{1,89}$ = 4·88* (0·0001, 0·00005)
Release order	$F_{1,46}$ = 0·62	$F_{1,44}$ = 0·31		
Sex	–	–		$F_{1,89}$ = 1·16
Streamer width × Elongation	$F_{1,46}$ = 0·79	$F_{1,44}$ = 1·33		
Streamer width × Elongation^2	–	$F_{1,44}$ = 1·56		$F_{1,89}$ = 8·30** (0·0024, 0·001)
Streamer width × Body mass	–	–	$F_{1,93}$ = 5·15* (–0·0150, 0·006)	
Streamer width × Elongation^2 × Body mass	–	–		$F_{1,89}$ = 8·29** (–0·0005, 0·0001)
Streamer width × Elongation × Sex	–	–		$F_{1,89}$ = 4·96* (–0·0014, 0·0006)
Streamer width × Elongation^2 × Sex	–	–		$F_{1,89}$ = 5·21* (0·0001, 0·0001)
Elongation × BOS	–	–	$F_{1,93}$ = 4·33* (0·0002, 0·0001)	
BOS	–	–	$F_{1,93}$ = 3·01	
Body mass	–	–	$F_{1,93}$ = 0·32	$F_{1,89}$ = 2·37
Tail symmetry	–	–		$F_{1,89}$ = 6·81* (0·0040, 0·0015)

In parentheses we provide parameter estimates and their standard errors. BOS: composite measure for body size. *$P < 0·05$, **$P < 0·01$; –, not tested; blank, not significant.

quadratic elongation terms in interaction with streamer width were statistically insignificant, and hence were removed from the model. An identical approach for number of strings hit as a dependent variable led to a final model that, after removal of insignificant factors, contained significant effects of streamer width and tail elongation (both linear and quadratic elongation terms), and an interaction of streamer width with elongation squared (overall model $r^2 = 0·20$; $F_{10,93} = 4·83$, $P < 0·001$; Table 1). The model also had a positive and significant effect of tail fluctuating asymmetry on number of strings hit. Therefore, manoeuvrability variables were still predicted by a streamer width variable ('narrow-feathered' birds manoeuvred significantly better than 'broad-feathered' birds), once other possible effects had been controlled statistically (Table 1, Fig. 3).

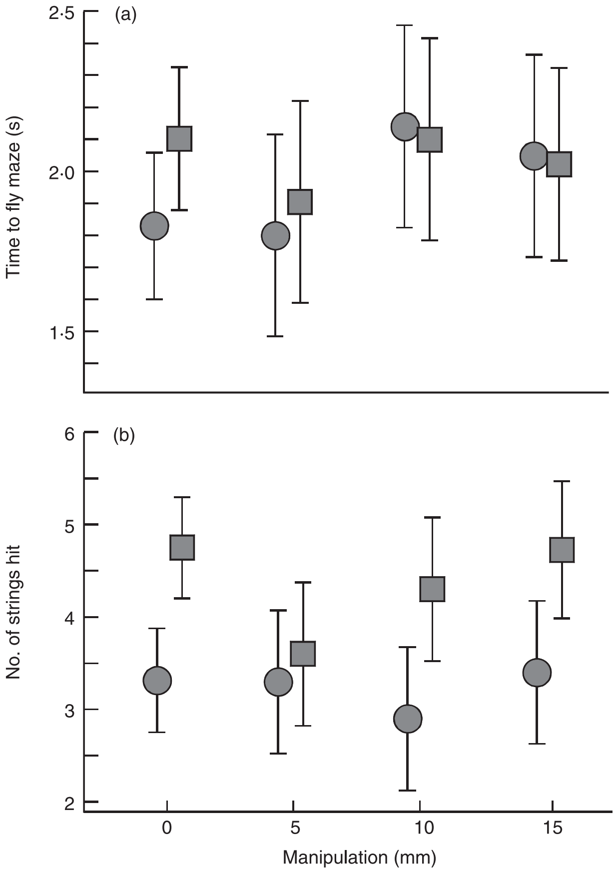

Fig. 3. The effect of mimicked tail elongation with broad (squares) and narrow (circles) pieces of feather on flight time through the maze test section (a) and the number of strings hit en route (b) in the house martin (Error bars = SE).

Discussion

As measured by the flight maze experiment, which mimicked the early stages of elongation of the outermost tail feathers in the house martin, 'narrow-feathered' birds (which had initial tail streamers modelled on a natural streamer of the barn swallow) negotiated the crowded maze environment more effectively than 'broad-feathered' birds, independent of the elongation of the feather. Next a small elongation of the outermost tail feathers (e.g. 5 mm elongation; B5 and N5 groups compared to B0 and N0 groups, respectively) did not improve manoeuvrability, both in the case of 'broad-feathered' or 'narrow-feathered' birds. Although a continuous tail elongation variable (both linear and quadratic elongation terms) significantly predicted manoeuvrability as measured by number of strings hit (Table 1), no significant differences existed among elongation group means. In terms of streamer

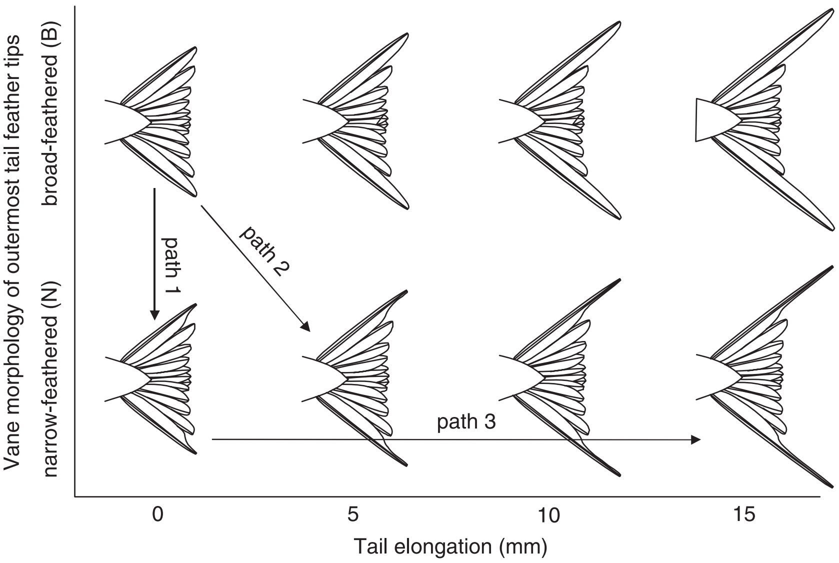

Fig. 4. Three hypothetical paths for evolution of hirundine tail streamers. Path 1, slender streamers evolve purely under natural selection for improved manoeuvrability through an evolutionary reduction of width and vane asymmetry of the outermost tail feather tips, without preceding elongation of tail feathers. Path 2, slender streamers evolve purely under natural selection for manoeuvrability through concurrent evolutionary narrowing and lengthening of the broad, vane asymmetric outermost tail feathers. Path 3, further evolutionary elongation of short slender streamers is not beneficial (nor detrimental) in the context of manoeuvrability; other evolutionary force, e.g. sexual selection, is necessary for the development of longer streamers.

evolution, the results suggest a natural selection advantage to narrowing the broad tips of outermost tail feathers in terms of improved manoeuvrability. By contrast, elongation of outermost tail feathers is not important in turning flight (unless in combination with feather narrowing; see below).

The results of the current study contrast with those obtained in previous studies (Park *et al.* 2000). In their experiments using narrow pieces of feather, Park *et al.* (2000) reported that a small streamer elongation improved manoeuvrability. Discrepancy between the results of these two studies may stem from differences in experimental protocols used. In Park *et al.* (2000), the control (no streamer) group had the outermost tail feathers with broad tips, from which the elongation of a narrow streamer began (as represented by consecutive elongation groups), while in the present study the control 'narrow-feather' (N0) group had already the outermost tail feather tips trimmed into a narrow streamer shape. In effect, while the present study investigated the effects of feather lengthening independent of those of feather narrowing on manoeuvrability, Park *et al.* (2000) have examined the aerodynamic effects of concurrent experimental lengthening and narrowing of the outermost tail feather tips into initial streamers. The positive effect of such a manipulation of the tail on manoeuvrability found by Park *et al.* (2000) was confirmed in the current study (see below).

Streamer-less hirundines may gain aerodynamic benefits in the context of manoeuvrability through the evolutionary narrowing of the broad tips of outermost tail feathers into slender streamers. This positive effect on manoeuvrability did not depend on the length of imitated streamers. It is plausible that initial streamers improved manoeuvrability in 'narrow-feathered' birds through the mechanism suggested by Norberg (1994). 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. It seems that this effect can function independent of the length of streamers (see Barbosa & Møller 1999) and thus can contribute to initial streamer evolution.

If there was selection for better manoeuvrability, the results of the current study suggest that streamers may evolve in streamer-less hirundines initially purely through natural selection. First, tail streamers might evolve through an evolutionary reduction of width of the outermost tail feather tips (an evolutionary transition from the 'broad-feathered' B0 stage to the 'narrow-feathered' N0 stage; path 1 in Fig. 4). Improved flight performance resulting from streamers could thus arise in the absence of preceding tail elongation (Matyjasiak *et al.* 2004). Such an initial streamer evolution would not impose costs to steady flight, elongated streamers having been shown to be detrimental to flight measures that are directly related to velocity and acceleration (Park *et al.* 2000). Because such streamers would not increase total tail area, then, according to theory (Thomas 1993), they would not increase aerodynamic drag generated from the tail.

Second, natural selection for improved manoeuvrability acting on a streamer-less hirundine species might lead to the evolution of even longer streamers through concurrent evolutionary lengthening and narrowing of the broad, vane asymmetric outermost tail feathers (e.g. an evolutionary transition from the 'broad-feathered' B0 stage to the 'narrow-feathered' N5 stage; path 2 in Fig. 4). This might happen when environmental conditions or prey composition changed such that the advantage of improved manoeuvrability exceeded the cost to other measures of flight performance (Park *et al.* 2000). It follows therefore, in contrast to the proposition by Møller *et al.* (1998) and Møller & Hedenström (1999), that sexual selection is not the only possible reason for the origin of swallow streamers. However, if there is no current selection for improved manoeuvrability, sexual selection must be invoked as the evolutionary pressure instigating the evolution of a long narrow streamer. We would like to point out that, like many other streamer-less hirundines, house martins have already evolved tails of a forked shape that is presumably aerodynamically optimal with respect to the lift : drag ratio (Thomas

1993). In such a tail, the broad-tipped outermost feathers could droop passively in the airflow to form a leading edge suction in a manner resembling the mechanism envisaged by Norberg (1994). Nonetheless, the addition of small narrow streamers to house martins improves manoeuvrability (see also Matyjasiak *et al.* 2004). Possible examples of extant bird species possessing short, narrow outermost tail feathers that might have been selected for manoeuvrability but not sexually selected are the common tern *Sterna hirundo*, Linnaeus and the arctic tern *Sterna paradisaea*, Pontoppidan.

Finally, the results of the current study suggest that further evolutionary elongation of the short slender streamer (an evolutionary transition from the 'narrow-feathered' N0 or N5 stage to the 'narrow-feathered' N10 or N15 stage) is not beneficial (nor detrimental) in the context of manoeuvrability (path 3 in Fig. 4). Similarly, we have found no aerodynamic advantages or costs in terms of manoeuvrability to be gained through the evolutionary elongation of the broad-tipped outermost tail feathers (an evolutionary transition from the 'broad-feathered' B0 stage to the 'broad-feathered' B5 or B10 stage). An elongation of the outermost tail feathers is detrimental to flight measures related to velocity and acceleration (Park *et al.* 2000) and impairs foraging success in streamer-less hirundines (Matyjasiak *et al.* 1999, 2000). Hence in both the 'narrow-feathered' and 'broad-feathered' stage, tail elongation under sexual selection is necessary for the development of longer streamers. In the latter case, a reduction in feather width might reduce feather area and thus decrease aerodynamic drag (Thomas 1993; Møller & Hedenström 1999). That we have not found a detrimental effect of further elongation of the initial streamer on flight manoeuvrability, similar to what was reported by Park *et al.* (2000), may stem from different methods used in these two studies. Park *et al.* (2000) measured flight performance in freely flying house martins, whereas in the present study birds were released into the flight maze that forced them to make increasingly tight turns and to manoeuvre at a maximum rate. Hence these two studies may have measured different aspects of manoeuvring flight, and hence their results may not be directly comparable.

Møller & Hedenström (1999) have found that all bird species with long sexually size-dimorphic tails consistently develop narrower tips of ornamental tail feathers with vanes of more equal width, as compared to closely related taxa with short size-monomorphic tails, independent of tail shape. Flight feathers such as wing primaries and secondaries, and tail feathers have asymmetric vanes (the outer vane being narrower than the inner vane), while body feathers have symmetric vanes (Norberg 1990). As vane asymmetry in combination with feather curvature and emargination is essential for an aerodynamic function of a feather as an aerofoil (Norberg 1985; Norberg 1990), loss of vane asymmetry is considered to indicate loss of aerodynamic function of a feather (Feduccia & Tordoff 1979). Aerodynamic drag, and therefore cost, of a feather is proportional to its area (Thomas 1993; but see Evans 2003), hence Møller & Hedenström (1999) attributed the evolution of slender feather tips with equally narrow vanes in species with sexually size-dimorphic tails to a general mechanism for reducing the aerodynamic cost of tail ornaments. The results of the current study argue against the hypothesis that the slender profile of streamers reflects loss of a function of these feathers in the context of flight performance. A reduction of the width and vane asymmetry of outermost feathers in forked tail ornaments can thus be considered not only a morphological modification reducing the aerodynamic disadvantage of elaborated feathers, but also an adaptation facilitating turning flight. The finding that improved manoeuvrability resulting from streamers may arise even in the absence of preceding elongation of outermost tail feathers (see also Matyjasiak *et al.* 2004) contradicts the proposition by Møller *et al.* (1998) and Møller & Hedenström (1999) that streamers in forked tails have evolved initially solely via sexual selection for costly signalling and only later on have aided manoeuvrability; that is, after the streamer had become long and narrow owing to cost-reducing modifications of vane morphology. Future research should focus upon the effect on flight performance of other aspects of finer morphology of tail feathers. Experimental studies could quantify the structural density and mechanical properties of tail streamers using the approach developed by Aparicio, Bonal & Cordero (2003) and Tubaro (2003), and measure the effect of these variables on manoeuvrability (birds might be tested in a flight maze and tail feathers might be measured afterwards).

Future research might also focus on the aerodynamics of the tail to update the theoretical work of Norberg (1994). Flight kinematics studies, for example, could manipulate width and length of the outermost tail feathers in living birds and evaluate the tail feather bending, twisting and rotation in a wind tunnel under different levels of upward action of airflow (aerodynamic load) and different angles of attack of the spread tail. At low air speed, the outermost tail feather tips in 'narrow-feathered' birds should control tail profile shape to a greater extent than in the case of 'broad-feathered' birds. The indirect aerodynamic function of tail streamers could be evaluated in various hirundine species in relation to other feather properties, such as shape, flexural stiffness and torsional rigidity of the feather shaft. Comparative studies of tail aerodynamics in different hirundines should consider streamer morphology as well as internal anatomical structures responsible for tail movements, such as the muscular arrangement and neuromuscular system (Moreno & Møller 1996). The latter issue was not evaluated in the present study. Modern streamer-less species may have tail muscular support and neuromuscular systems different from the supposed ancestors that gave rise to streamer-tailed species. This would mean that the current model of tail streamer evolution leaves some uncertainty about how different streamer-less hirundines would perform given incipient stages of tail feather elongation. However, like barn swallows, house martins have long skeletal tails enabling them to develop relatively great force in order to counteract the upward action of air flow (Moreno & Møller 1996). This might allow them to take a mechanical advantage of tail streamers and to generate more lift from the tail allowing for tighter turns, which is consistent with the results of this study.

In conclusion, in the house martin narrowing of the broad tips of outermost tail feathers into slender streamers augments manoeuvrability, and thus may provide a natural selection advantage in terms of improved flight performance. Elongation of narrow streamers does not improve turning flight, however, unless in combination with feather narrowing. These results suggest that streamers are most likely to have evolved in the first instance via natural selection for improved manoeuvrability. As it is the narrowness and not elongation of the outermost tail feathers that is important for manoeuvrability, then, contrary to Park *et al.* (2000), streamer elongation is better explained by the sexual-selection than the improved-manoeuvrability hypothesis.

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