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4 Assessing the aerodynamic effects of tail elongations
5 in the house martin (*Delichon urbica*):

6 Implications for the initial selection pressures in hirundines

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19 Word count: 5, 844 inc. references

20 Key words: Flight performance, hirundines, natural selection, sexual selection, tail streamers.

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22
23 **Abstract** Of the three species of Hirundine that breed sympatrically across the U.K., one, the
24 barn swallow, has outer tail feathers elongated into streamers, whereas the other two species, the

25 house martin and the sand martin, do not. The tail streamer of the barn swallow is regarded as a
26 classic example of a sexually selected trait. Recent evidence, however, has suggested that
27 streamers may have evolved largely through natural selection for enhanced flight performance
28 and increased maneuverability. We tested the hypotheses that small streamers 1) increase
29 performance in turning flight, but 2) decrease performance in flight variables related to velocity.
30 We manipulated the lengths of house martin outer tail feathers and measured changes in their
31 free-flight performance, using stereo-video to reconstruct the birds' 3D flight paths. Five flight
32 variables were found to best describe individual variation in flight performance. Of these five,
33 the three variables determining maneuverability predicted that flight performance would be
34 optimized by a 6 to 10mm increase in the length of the outer tail feathers. In contrast, for mean
35 velocity and mean acceleration, extension of the outer tail feathers appears to have a detrimental
36 effect on flight performance. We suggest that the initial selection pressure for streamers in
37 ancestral short-tailed 'barn swallows' was via natural selection for increased maneuverability. In
38 addition, we propose that the benefits of increased maneuverability has differed between
39 hirundines in the past, such that the cost of increasing the length of the outer tail feather has, to
40 date, outweighed the benefits of doing so in streamer-less hirundines.

41

42 **Introduction**

43

44 The traits of many animals fulfill several important functions. The assumption is that the current
45 observed size of such traits is the fitness optimum. However, this may not be the optimum for
46 each, or any, of the trait's separate functions. In addition, some traits would appear to have no
47 survival advantages for the bearer, and Darwin (1871) suggested sexual selection as a mechanism
48 for the development of such traits. In the last 20 years there has been considerable interest in the
49 possible trade-offs between natural and sexual selection pressures (Andersson 1994). Avian tail

50 morphology represents a good example of trade-offs between multiple functions as tails may
51 have several uses (Balmford et al. 1993). Theory predicts that different modes of flight (e.g.
52 migratory flight, foraging flight) would select for different optimal tail designs (Thomas 1995).
53 Tails are also used for signaling and during mate choice, and these functions will produce
54 different selection pressures on the tail than will aerodynamic functions (Balmford et al. 1993).
55
56 Many hirundines (Hirundinidae) possess elongated outer tail feathers (streamers), and it appears
57 that this trait has evolved at least twice (Møller 1994), although the initial evolutionary pressures
58 for streamers are unknown (but see Matyjasiak et al. 2000; Rowe et al. in press). The three
59 species that breed around the study sites used here are sympatric across their range: barn
60 swallows (*Hirundo rustica*) have streamers while house martins (*Delichon urbica*) and sand
61 martins (*Riparia riparia*) do not. Male barn swallows have streamers which are approximately
62 16% longer than those of females (Møller 1988). Females preferentially mate with males that
63 have long streamers, so long-tailed males benefit from a higher annual reproductive success
64 (Møller 1988; Smith and Montgomerie 1991). The streamer of the male barn swallow has been
65 regarded as a classic example of a secondary sexually selected trait (Møller 1994) since,
66 theoretically, the streamer impairs aerodynamic performance through increased drag (Thomas
67 1993). Only high quality males are able to withstand this handicap and it has been found, for
68 example, that long-tailed males have higher survival rates and reduced parasitism levels (Møller
69 1989; Møller and de Lope 1994). More recently, however, it has been proposed that streamers
70 may to some extent, aid aerodynamic performance (Norberg 1994). Because of the aeroelastic
71 properties of the outer tail feather the streamer bends upwards and backwards which creates a
72 vortex flap at the front edge of the tail. This flap helps prevent flow separation, thereby delaying
73 stalling to higher angles of attack and allowing the bird to perform tighter turns, so improving
74 maneuverability (Norberg 1994). To date, the sexual selective advantages of possessing

75 streamers have been extensively studied (Møller 1994), but the aerodynamic effects of such a
76 trait have not (but see Buchanan and Evans 2000).

77

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

94

95 We can also use aerodynamic theory to predict changes in flight performance after the addition
96 of a small streamer to hirundine species that lack this trait. If the initial selection pressure
97 promoting the evolution of tail streamers was enhanced aerodynamic performance (via natural
98 selection), adding a small streamer would result in an initial increase in flight performance,
99 followed by a decrease after the optimum length is exceeded. If, however, the initial selection

100 pressure was sexual selection, any increase in the length of the outer tail feather would result in a
101 continuous decrease in flight performance. House and sand martins are ideal subjects for such
102 studies because they do not possess streamers and mate choice is unlikely to be an influencing
103 factor in tail evolution as the tails of males and females are morphologically similar. Presumably
104 then, tail morphology in these species is at its naturally selected optimum. Rowe et al. (in press)
105 found that the addition of small streamers (up to 20mm) to sand martins increased flight
106 maneuverability, indicating that species without streamers could gain some aerodynamic benefit
107 from the evolution of small streamers. This indicates, as suggested by Norberg (1994) that the
108 initial selection pressure for streamers in the short-tailed ancestor of the barn swallow may have
109 been via natural selection for increased maneuverability. However, it is not known whether this
110 is traded off against detrimental effects on flight variables other than maneuverability.

111

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

124

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

135

136 **Methods**

137

138 Male and female house martins were caught while roosting in artificial nest boxes at two
139 breeding sites in Central Scotland in 1998 and 1999. The following biometric measurements
140 were taken; left and right wing length (maximum chord), left and right outer tail feather length,
141 and the length of the mid-tail feather were measured to the nearest millimeter with a ruler; head
142 and bill length was measured to the nearest 0.1mm using vernier calipers; body mass was
143 measured to the nearest 0.1gram using a pesola spring balance. Paired measurements were
144 averaged to calculate mean wing and outer tail length. Repeatability estimates (intra-class
145 correlation coefficient, r_i) for these measurements were calculated (Lessels and Boag 1987) using
146 individuals caught more than once. Mean wing length ($F_{17,18} = 13.60, p < 0.001, r_i = 86\%$), mean
147 outer tail feather length ($F_{20,21} = 22.81, p < 0.001, r_i = 92\%$), mid-tail feather length ($F_{20,21} =$
148 $5.56, p < 0.001, r_i = 69\%$), and head and bill length ($F_{20,21} = 3.59, p < 0.001, r_i = 56\%$) were
149 significantly repeatable. Body mass ($F_{20,21} = 1.98, \text{NS}, r_i = 33\%$) was not significantly repeatable.

150 Sex was determined by presence (female) and absence (male) of a brood patch (Svensson 1992).
151 Before release, individuals were marked on the breast and rump with a unique combination of
152 dyes (Pantone Inks, Letraset) so they could be identified in the field.
153
154 Marked birds were filmed flying towards and away from nest boxes using two Sony cameras
155 (Sony Digital Handycam DCR - VX1000E) mounted 1m apart on a rigid bar. The cameras were
156 aligned at 90° to the mounting bar which was held level. The stereo-video technique allows the
157 reconstruction of 3D flight paths which can be used to calculate various measures of free-flight
158 performance (Evans 1998; Buchanan and Evans 2000; Evans, Buchanan and Park
159 (unpublished)). Once birds had been filmed they were recaptured and randomly allocated to one of
160 two experimental groups (6mm or 15mm streamer), or a control group (no streamer). Birds in the
161 experimental groups had the two outer tail feathers cut to within 10mm of the base and replaced
162 with outer tail feathers from a swallow which were butted onto the feather shaft and fixed by the
163 insertion of a 5mm wire pin (0.6mm gauge, < 10mg) into the pulp cavity of the rachis (Smith and
164 Montgomerie 1991; Matyjasiak et al. 1999). Cyanoacrylic superglue was used to hold the pin in
165 place. The outer tail feathers were then trimmed to a natural streamer shape 6mm or 15mm
166 longer than the length of the original tail feather (Fig. 1). Birds in the control group had same
167 length of wire fixed to the base of the outer tail feathers with cyanoacrylic superglue to control
168 for the weight of the wire. Manipulated birds were then re-filmed. Filming took place between 1
169 and 7 days after manipulation. Multiple flight sequences were obtained for each bird, and an
170 average value for the flight variables before and after manipulation was calculated. These
171 variables will be referred to in the subsequent text as the initial flight variables (before
172 manipulation) and final flight variables (after manipulation).

173

174 The stereo-video footage was digitized using the miroMOTION DC20 digitizer (Pinnacle
175 Systems, Middlesex, UK) on an Apple Macintosh 9500. The digitized footage was then edited
176 using Adobe Premiere 4.0 (Adobe Systems Incorporated) and the 2D co-ordinates of the center
177 of the bird's body (on both the left and right camera) were obtained from each frame using the
178 public domain NIH image program (available on the internet at [http://rsb.info.nih.gov/nih-](http://rsb.info.nih.gov/nih-image/)
179 [image/](http://rsb.info.nih.gov/nih-image/)). The focal length of the camera, camera separation and the stereo-pairs of 2D co-
180 ordinates were then used by a computer program to obtain the 3D co-ordinates for the flight path.
181 The 3D co-ordinates were smoothed using a fourth difference algorithm (Rayner and Aldridge
182 1985), and used to calculate flight variables for individual flight paths; mean, minimum and
183 maximum velocity; mean, minimum and maximum acceleration; mean and maximum energy
184 (sum of potential and kinetic); mean and maximum curvature; mean and maximum rate of
185 change of curvature; mean and maximum curvature in the XY plane; mean and maximum rate of
186 change of curvature in the XY plane; mean, minimum and maximum turn radius, mean and
187 maximum agility. The XY plane represents the vertical 2D plane running parallel to the cameras.
188 For details of how these variables are calculated refer to Rayner and Aldridge (1985), Buchanan
189 and Evans (2000), and Evans, Buchanan and Park (unpublished). The error (accuracy) associated
190 with these measurements was estimated by plotting the co-ordinates for a stationary object 1m in
191 length and calculating the error in the positional data which was 8.0 % (s.e. ± 0.51 , $n = 207$). The
192 errors associated with the calculation of the flight variables are discussed in Evans, Buchanan
193 and Park (unpublished) and are all under 10%. All filming and digitizing were carried out blind
194 to the manipulation group of the bird being filmed.

195

196 Data were transformed to achieve normality and analyzed using MINITAB release 12.1 and
197 SPLUS 4.5. As the 21 flight variables calculated do not vary independently they were reduced to
198 the smallest set of independent variables that explained significant covariation in the others (see

199 also Buchanan and Evans 2000). Only initial flight variables (i.e. before manipulation) were used
200 for this analysis to avoid each bird being considered twice. Mean velocity was found to explain
201 significant variation in the largest number of variables. Flight variables not explained by mean
202 velocity were added to it sequentially and multiple regression was used to find which
203 combination of two variables explained significant variation in the largest number of remaining
204 variables. This process was continued until all the flight variables were explained by the smallest
205 set of independent predictor variables. Five flight variables were found which best explained
206 most individual variation; mean velocity, mean acceleration, maximum curvature, maximum
207 curvature in the XY plane, and maximum rate of change of curvature in the XY plane. Curvature
208 is a scalar measure of the deformation of the flight path, and therefore provides quantitative
209 information on maneuverability. Curvature in the XY plane is a component of this measurement,
210 and is an important measure of performance in a level turn (Rayner and Aldridge 1985). The
211 term performance is used in this paper in relation to an individual's behavioral strategy, and is
212 not intended to infer that particular flight characteristics are more desirable than any other.

213

214 We have taken two approaches to the analysis of these data, which differ only in the degree of
215 complexity of the statistical models (General Linear Model ANOVA) constructed:

216

217 1) A simple model was constructed for each of the five flight variables, with the final flight
218 variable as the dependent variable. Only year, site (factors), the initial flight variable, and
219 the variable of interest, manipulation and manipulation² (covariates), were included in these
220 models. If the quadratic term manipulation² did not explain a significant amount of
221 variation in the final flight variable, it was removed in order to assess the importance of the
222 linear term manipulation to the model.

223

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

232
233 The residuals were checked at each stage for a normal distribution and homoscedasticity. The
234 regression coefficients of the complex stepwise GLM were used to produce the equation of the
235 line relating final flight variable to manipulation. Where a curvilinear relationship was found
236 between final flight variable and manipulation the maximum/minimum point was determined by
237 differentiation of the regression coefficients. The maximum/minimum point on a curve can be
238 defined as $df/dx = 0$, that is the manipulation size at which the rate of change of the function
239 becomes zero. Using bootstrapping, a population of maximum/minimum points was generated
240 from the original dataset allowing 95% confidence intervals and interquartile ranges to be
241 estimated.

242
243 For a comparison of maneuverability between barn swallows and house martins, the minimum
244 turn radius of unmanipulated barn swallows (from Buchanan and Evans 2000) filmed using the
245 same equipment and analyzed using the same technique was compared to that of unmanipulated
246 house martins under similar flight conditions (commuting flight: flying towards and away from
247 nest sites).

248

249 **Results**

250

251 Flight sequences before and after manipulation were obtained for 16 house martins. Repeatability
252 estimates of final flight variables were calculated from between 3 and 21 flight sequences for the
253 same individual ($n = 16$). The r_i values are presented alongside F ratios and p values calculated
254 in the ANOVA. Most flight variables were significantly variable between individuals. Mean
255 velocity ($F_{15,99} = 24.35, p < 0.001, r_i = 77\%$), mean acceleration ($F_{15,101} = 1.94, p < 0.05, r_i =$
256 12%), maximum curvature ($F_{15,101} = 3.42, p < 0.001, r_i = 25\%$), maximum curvature in the XY
257 plane ($F_{15,98} = 2.46, p < 0.01, r_i = 17\%$), and maximum rate of change of curvature in the XY
258 plane ($F_{15,97} = 2.85, p = 0.001, r_i = 21\%$) were all significantly repeatable.

259

260 Relationship between flight performance and addition of streamers

261

262 Results from the simple General Linear Models (Table 1) show that maximum curvature,
263 maximum curvature in the XY plane and maximum rate of change of curvature in the XY all had
264 significant curvilinear relationships with tail manipulation. In contrast, the relationship between
265 mean velocity and mean acceleration with manipulation was best described with a negative linear
266 function. The complex models, containing sex, morphological variables and interactions, show a
267 similar pattern: of the five independent flight variables, four were found to have significant
268 curvilinear relationships with tail manipulation, either alone (mean velocity, maximum curvature,
269 maximum curvature in the XY plane) or in an interaction with sex (maximum rate of change of
270 curvature in the XY plane) (Fig. 2; Table 2). The fifth independent flight variable - mean
271 acceleration - had a negative linear relationship with tail manipulation. All results presented from
272 here on relate to those derived from the complex models. To determine the optimal streamer
273 length for each flight variable showing a curvilinear relationship with tail manipulation, the

274 position of the maximum/minimum point was calculated using the regression coefficients from
275 the models (Table 3). The maximum/minimum points for all of the four quadratic relations were
276 greater than zero and ranged from 6.16mm to 9.78mm (Table 3). The maximum/minimum point
277 for mean velocity was 9.78mm although this is not obvious from Fig. 2a, in part due to the
278 significant interaction between manipulation and outer tail feather length (Table 2). The
279 interaction indicates that the effect of tail manipulation varies with the original length of the
280 outer tail feather. The data in Fig. 2a represents the effect of tail manipulation on velocity with an
281 average tail length of 60.87mm. Data from the General Linear Models were used to calculate a
282 population distribution of maximum/minimum points using bootstrapping (1000 replicates)
283 (Table 3). Confidence intervals (upper and lower 95%) and interquartile ranges (25% and 75%)
284 were calculated. Confidence intervals describing the optimum outer tail feather length for mean
285 velocity were extremely wide, with values exceeding ± 1000 mm (Table 3). This is explicable as
286 the relationship between mean velocity and manipulation is virtually linear: The percentage of
287 replicates for mean velocity with maximum/minimum points between 0 and 20mm (a range
288 which we consider represents a “small streamer”) was very low (5%). This indicates that the
289 curve for the effect of manipulation on mean velocity is extremely shallow. In contrast,
290 confidence intervals for the measures of curvature were considerably tighter than this and ranged
291 from -2.83 to +15.00mm (Table 3). The percentage of replicates with maximum/minimum points
292 between 0 and 20mm was far higher than for mean velocity: maximum curvature (89%),
293 maximum curvature in the XY plane (89%), and maximum rate of change of curvature (female =
294 70%, male = 64%).

295
296 The influence of the quadratic (manipulation²) term upon the flight variables can be illustrated by
297 comparing the R² (proportion of variance explained) of each model with and without the
298 quadratic term (Table 4). The percentage change in R² caused by the removal of the quadratic

299 term is small for mean velocity (7%). However, the quadratic term has a larger effect on
300 maximum curvature, maximum curvature in the XY plane, and rate of change of curvature in the
301 XY plane as its removal results in a reduction of the R^2 by 56%, 16% and 13% respectively.
302 Again, this indicates that, in contrast with the curves from the other flight variables, the curve for
303 the effect of manipulation on mean velocity is extremely shallow.

304

305 Comparison of maneuverability between barn swallows and house martins

306

307 The comparison of barn swallow turning flight with that of unmanipulated house martins under
308 similar conditions showed that barn swallows had significantly smaller turn radii than house
309 martins, that is they performed tighter turns in flight than did house martins (t-test, $T_{6,16} = 3.96$, p
310 < 0.01 ; Fig. 3).

311

312 **Discussion**

313

314 Impact of streamers on flight performance

315

316 Both the simple and the complex models presented for this study show, as predicted, curvilinear
317 relationships for flight variables determining maneuverability (maximum curvature, maximum
318 curvature in the XY plane, and maximum rate of change of curvature in the XY plane). This
319 experiment has shown that the flight performance of house martins during turning flight is
320 optimized by a 6 to 10mm increase in the length of the outer tail feathers. This demonstrates that
321 flight performance in turning flight increases with the addition of a small streamer up to an
322 optimal length, and then decreases once the optimal length has been exceeded. Due to the wide
323 confidence intervals, the exact position of the optimal streamer length for maneuverability is

324 unclear (Table 3), possibly in part due to the small sample size of this study. However, the high
325 percentage of replicates that had an optimum between 0-20 mm indicates the high probability
326 that the aerodynamic optimum for maneuverability in house martin tails lies within this region.

327

328 The position of the maximum/minimum point on a quadratic function can either be the minimum
329 point of a U-shaped curve, or the maximum point of an \cap -shaped curve (Evans and Thomas
330 1987). Examination of the maximum rate of change of curvature in the XY plane showed that
331 there were differences between males and females in regard to the form of the quadratic function,
332 with males displaying a U-shaped response to manipulation, and females an \cap -shaped response.

333 The position of the maximum/minimum point was, however, very similar (6.2 and 8.8mm
334 respectively). The reason for these differences is unclear but it should be stressed that the sample
335 sizes involved in a comparison of the sexes were very small, and more data are required if this
336 result is to be interpreted with any confidence.

337

338 Mean velocity and mean acceleration had negative linear relationships with manipulation (simple
339 model), but there was a significant curvilinear relationship of mean velocity with manipulation in
340 the complex model. In this model, however, the wide confidence intervals, low percentage of
341 replicates with a maximum/minimum point between 0 and 20mm, and the low R^2 of the quadratic
342 term indicate that although there was a significant quadratic relationship between mean velocity
343 and tail manipulation, the curve is an extremely shallow one and is probably of limited biological
344 significance. The relationship between mean velocity and manipulation, therefore, could
345 essentially be considered a negative linear one, mean velocity decreasing with manipulation size
346 over the region of interest. The decrease in velocity and acceleration with the addition of small
347 streamers is consistent with models of minimum power and maximum range speed changes for
348 scarlet-tufted malachite sunbirds with elongated tails (Evans and Thomas 1992). It is not obvious

349 whether this decrease in velocity and acceleration can necessarily be interpreted as detrimental to
350 the bird's flight. The alternative is that this decrease is beneficial to the bird's flight but that the
351 optimum length of streamer exceeds the maximum manipulation used here (15mm). We believe,
352 however, that it is unlikely that adding a streamer of much over 15mm would have a beneficial
353 effect on these measures of flight performance as this species lack any of the traits, such as
354 longer wings, that have coevolved with streamers.

355

356 In summary, the addition of small streamers to house martins has a range of effects on different
357 aspects of flight performance: for variables determining maneuverability outer tail feather length
358 is optimized by a 6 to 10mm increase. In contrast, for variables such as velocity and acceleration,
359 outer tail feathers are probably at their optimum length and increasing their length appears to
360 have a detrimental effect on flight performance. These results are consistent with the predictions
361 made by Thomas (1993) who stated that any extension of the tail beyond the maximum
362 continuous span would increase drag and not lift. In addition, during straight flight when the tail
363 is furled, the Norberg mechanism would not be able to operate and streamers are likely only to
364 add to drag.

365

366 Evolutionary selection pressures on streamer development in hirundines

367

368 The results from this experiment suggest that hirundines may gain some aerodynamic benefit in
369 terms of maneuverability through the evolution of streamers. This result is consistent with recent
370 work testing the maneuverability of sand martins with manipulated tails length in a flight maze
371 (Rowe et al. in press). That two species of streamer-less hirundine should react to tail
372 manipulation in a similar way using entirely different methods of measuring flight performance
373 indicates that this result is robust. Interestingly, Rowe et al. (in press) found that the optimal

374 streamer length in sand martins exceeded the maximum 20mm manipulation used in that
375 experiment. Other than the different species being investigated, the explanation to this apparent
376 contradiction with our findings may lie in the different techniques used. Sand martins in that
377 study were released into a flight maze which forces the birds to make very tight maneuvers
378 around obstacles, whereas house martins in this study were free-flying. We were, therefore,
379 investigating a different type of flight performance that may not be directly comparable. That
380 streamer evolution has not occurred in many species of hirundine, including house martins and
381 sand martins, suggests that there maybe some selection pressure preventing streamer evolution.
382 We suggest that this pressure may arise from the detrimental effect that initial streamer evolution
383 has on aspects of flight performance relating to velocity and acceleration.

384

385 In summary, there is now considerable evidence that the addition of streamers to streamer-less
386 hirundines improves maneuverability in turning flight. This suggests that initial streamer
387 evolution in ancestral barn swallows may have evolved through natural selection for
388 maneuverability. We have shown quantitatively that barn swallows are more maneuverable than
389 house martins during commuting flight (Fig. 3). The underlying mechanism behind the initial
390 improvement in performance is, however, unclear. Norberg (1994) suggested that the evolution
391 of tail streamers may have promoted increased maneuverability during turning flight. This
392 mechanism relies on the aeroelastic properties of the streamer which presumably differ with
393 changes in length. Whether this mechanism can operate at the short streamer lengths used in this
394 experiment remains unknown. However, it is likely that there is a monotone, increasing function
395 describing the enhancement of lift and decrease of drag that would follow upon a lengthening of
396 a streamer of the outer tail feather (Norberg pers comm.). Thomas (1993) postulated that in flight
397 a bird's tail would bend, and that as pressure is not distributed evenly over the surface, the outer
398 tail feathers would be subjected to a component of lateral pressure. This results in the leading

399 edges of the tail drooping in a similar way to that proposed for the Norberg mechanism (Thomas
400 1993). If this theory is correct it is possible to envisage how streamers might operate under the
401 Norberg mechanism even at small lengths.

402

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

412

413 Tail morphology and flight performance in hirundines

414

415 By manipulating tail length and filming house martins in flight we have been able to differentiate
416 between different aspects of their flight performance. We have shown that, as predicted, flight
417 variables differ in their response to increased outer tail feather length. Nesting behavior may also
418 have influenced streamer evolution: barn swallows build open nests which allow their streamers
419 to hang outside of the nest, whereas house martins build closed nests and sand martins nest in
420 burrows. If this nesting behavior resulted in large asymmetries, from wear and tear on the
421 streamer, maneuverability would be reduced to below that seen in the absence of streamers
422 (Thomas 1993). Assuming house martin tail morphology is at an overall optimum it would
423 appear that the advantage of increased maneuverability is outweighed by the cost of streamers on

424 other aspects of flight performance, and possibly on the species ecology and life history. If
425 environmental conditions altered such that the benefit of increased maneuverability surpassed the
426 cost on other factors, we suggest that streamers may evolve in species currently without them.

427

428 **Acknowledgements**

429

430 The first version of the flight program was written by Adrian Thomas. Thanks to Alasdair
431 Sherman for his help with the equipment and fieldwork, and to the local householders who gave
432 us permission for access to the sites. This work was funded by NERC grant GR3/10600. We
433 thank R Gibson, R.Å. Norberg and an anonymous referee for comments on the manuscript.

434

435 **References**

436

437 Andersson M (1994) Sexual selection. Princeton University Press

438 Balmford A, Thomas ALR, Jones IL (1993) Aerodynamics and the evolution of long tails in
439 birds. *Nature* 361:628-631.

440 Buchanan KL, Evans MR (2000) The evolution of tail streamers in barn swallows. *Behav Ecol*

441 Darwin C (1871) *The descent of man and selection in relation to sex*. Murray, London

442 Evans MR (1998) Selection on swallow tail streamers. *Nature* 394:233-234

443 Evans MR (1999) Length of tail streamers in barn swallows - reply. *Nature* 397:115-116

444 Evans, MR, Thomas ALR (1992) The aerodynamic and mechanical effects of elongated tails in
445 the scarlet-tufted malachite sunbird: measuring the cost of a handicap. *Anim Behav* 43:337-
446 347.

447 Evans MR, Thomas ALR (1997) Testing the functional significance of tail streamers. *Proc Roy*
448 *Soc Lond B* 264:211-217

449 Hedenström A, Møller AP (1999) Length of tail streamers in barn swallows. *Nature* 397:115

450 Lessels CM, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. *Auk* 104:116-121

451 Matyjasiak P, Jabłoński PG, Olejniczak I, Boniecki PI (2000) Imitating the initial evolutionary
452 stage of a tail ornament. *Evolution* 54:704-711

453 Matyjasiak P, Jabłoński PG, Olejniczak I, Boniecki PI, Lee SD (1999) Foraging cost of a long
454 tail ornament: an experiment with sand martin females. *Ethology* 105:521-530

455 Møller AP (1988) Female choice selects for male sexual tail ornaments in the monogamous
456 swallow. *Nature* 332:640-642

457 Møller AP (1989) Viability costs of male tail ornaments in a swallow. *Nature* 339:132-135

458 Møller AP (1994) *Sexual selection and the barn swallow*. Oxford University Press, Oxford

459 Møller AP (1996) The cost of secondary sexual characters and the evolution of cost-reducing
460 traits. *Ibis* 138:112-119

461 Møller AP, de Lope F (1994) Differential costs of a secondary sexual character: An experimental
462 test of the handicap principle. *Evolution* 48:1676-1683

463 Norberg RA (1994) Swallow tail streamer is a mechanical device for self-deflection of tail
464 leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proc Roy Soc*
465 *Lond B* 257:227-233

466 Rayner JMV, Aldridge HDJN (1985) Three-dimensional reconstruction of animal flight paths
467 and the turning flight of microchiropteran bats. *J Exp Biol* 118:247-265

468 Rowe LV, Buchanan KL, Evans MR (in press) The function and evolution of the tail streamer in
469 the barn swallow. *Behav Ecol*

470 Smith HG, Montgomerie R (1991) Sexual selection and the tail ornaments of North American
471 barn swallows. *Behav Ecol Sociobiol* 28:195-201

472 Svensson L (1992) *Identification guide to European passerines* (4th edn). Svensson, Stockholm

473 Thomas ALR (1993) On the aerodynamics of birds' tails. *Phil Trans Roy Soc Lond* 340:361-380

474 Thomas ALR (1995) On the tails of birds. PhD thesis. University of Lund, Sweden
475 Thomas ALR (1996) The flight of birds that have wings and a tail: variable geometry expands
476 the envelope of flight performance. *J Theor Biol* 183:237-245
477 Turner A, Rose C (1989) A handbook to the swallows and martins of the world. Christopher
478 Helm, London
479 Waugh DR (1978) Predation strategies in aerial feeding birds. PhD thesis. University of Stirling,
480 UK

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493 **Figure legends**

494

495 **Fig. 1**

496 Unmanipulated (**a**) and manipulated (+15mm) (**b**) house martin outer tail feathers. Birds in the
497 experimental groups (+6 and + 15mm) had the two outer tail feathers cut to within 10mm of the
498 base (indicated by the horizontal lines across the feather) and replaced with outer tail feathers

499 from a swallow which were butted onto the feather shaft and fixed by the insertion of a 5mm
500 wire pin (0.6mm gauge, < 10mg) into the pulp cavity of the rachis. Cyanoacrylic superglue was
501 used to hold the pin in place. The outer tail feathers were trimmed to give a natural rounded end,
502 and at the side in order that it graduates in accordance with the other tail feathers (i.e. trailing
503 edges overlap). Care was taken to ensure that the feather vane of the manipulated feather was
504 adjusted during manipulation so that it lay in the same plane as the tail.

505

506 **Fig. 2**

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

524

525 **Fig. 3**

526 Comparison of minimum turn radius (commuting flights) between unmanipulated barn swallows
527 ($n = 10$) and house martins ($n = 16$). Box plots shown here indicate the 10th, 25th, 50th, 75th and
528 90th percentiles with horizontal lines and all data points outside this range.

529

530

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	mean velocity	mean acceleratio n	maximum (max) curvature	max. xy curvature	max. 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	$F_{1,11} = 5.42^*$	$F_{1,11} = 4.64^*$	$F_{1,10} = 4.64$	$F_{1,10} = 12.10^{**}$	$F_{1,10} = 8.04^*$
manipulation²	-	-	$F_{1,10} = 4.96^*$	$F_{1,10} = 8.89^*$	$F_{1,10} = 5.96^*$

Table I Results from the simple General Linear Models for each flight variable examined. Effects of streamer addition (manipulation and manipulation²), initial flight variable, site and year are shown. If the quadratic term manipulation² 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. * = $p < 0.05$, ** = $p < 0.01$.

	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)²	$F_{1,4} = 41.80^{**}$		$F_{1,10} = 4.96^*$	$F_{1,10} = 8.89^*$	$F_{1,6} = 0.75$
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)²					$F_{1,6} = 6.00^*$
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	$F_{1,4} = 21.2^*$				

Table II Results from the complex General Linear Models for each flight variable examined. Effects of streamer addition (manipulation and manipulation²), initial flight variable, sex, site, year, the interaction terms and morphological variables on individual variation 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. * = $p < 0.05$, ** = $p < 0.01$.

	mean velocity	maximum curvature	maximum curvature in XY plane	maximum rate of change of curvature in XY plane (female)	maximum rate of change of curvature in XY plane (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	-1023.83	-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	1288.50	11.50	15.00	11.25	11.50

Table III Position of the maximum/minimum (mm) for each flight variable with a significant manipulation² term (quadratic function), calculated from the ANOVA coefficients, and the distribution of turning points derived from bootstrapping showing the median, upper and lower 95% confidence intervals and upper and lower quartiles.

	mean velocity	mean acceleration	maximum curvature	maximum curvature in XY plane	maximum rate of change of curvature in XY plane
model R²	99.29	81.50	53.17	80.67	89.23
model excluding (manipulation)² R²	91.82	81.50	29.93	63.47	77.12
% reduction in R²	7.52 0.5>p>0.25	0	43.70 0.05>p>0.025	21.31 0.1>p>0.05	13.58 0.2>p>0.1

Table IV Effect of the manipulation² term (quadratic function) on the R² (variance explained) of the final model. The R² of the model before and after the removal of the quadratic function are shown along with the percentage reduction in R² (and the p value for the size of the absolute reduction in R²).

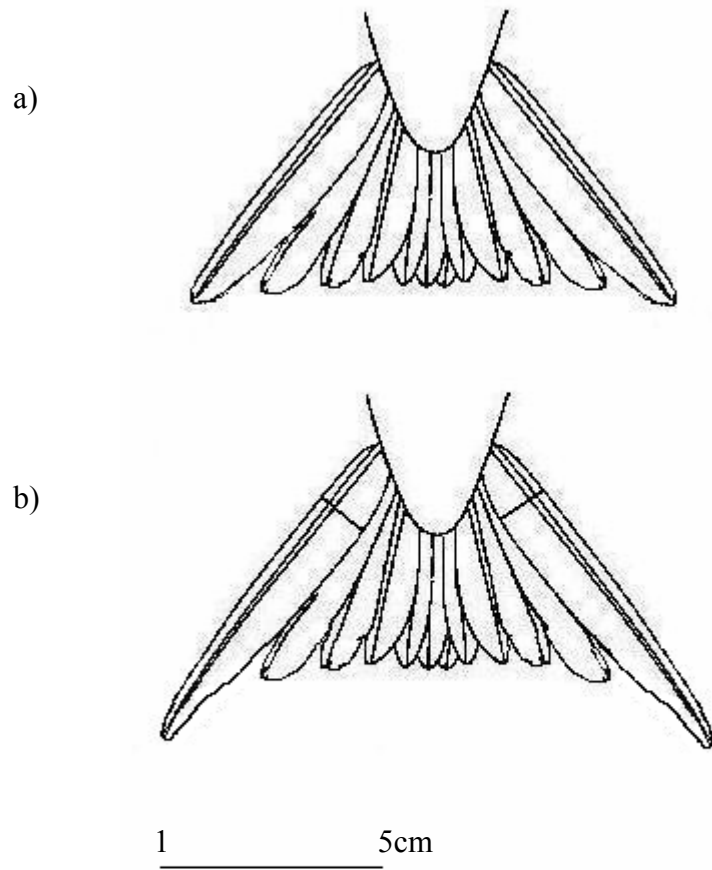


Fig. 1 Park, Evans and Buchanan

Fig. 2 Park, Evans and Buchanan

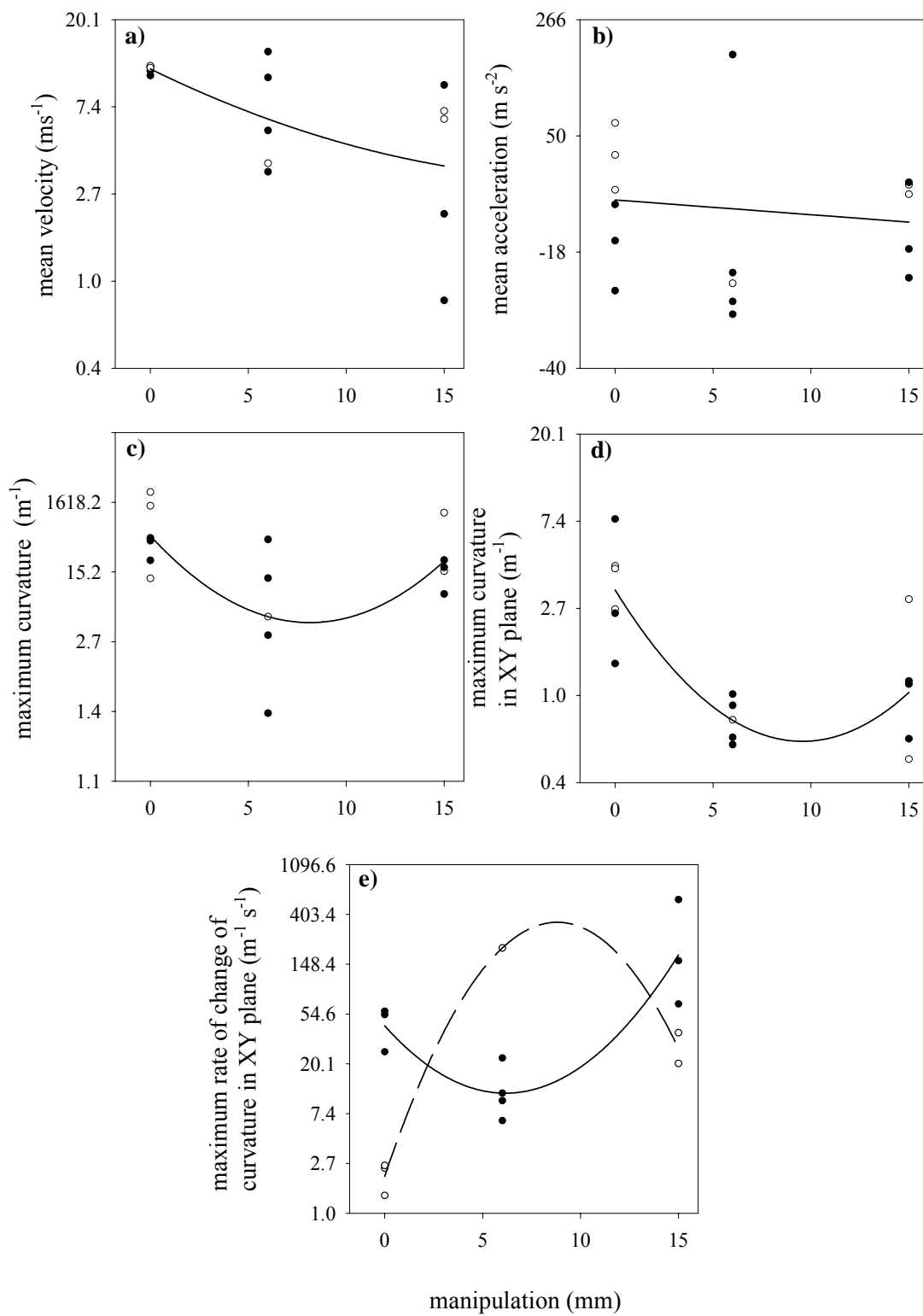


Fig. 3 Park, Evans and Buchanan

