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# Assessing the aerodynamic effects of tail elongations

# in the house martin (*Delichon urbica*):

# Implications for the initial selection pressures in hirundines

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**Abstract**  Of the three species of Hirundine that breed sympatrically across the U.K., one, the

barn swallow, has outer tail feathers elongated into streamers, whereas the other two species, the

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**

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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

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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**

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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 ($F_{20,21} = 1.98$, 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 $90^o$ 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 recaught 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-

179    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. $\pm$ 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 manipulation$^2$ (covariates), were included in these

220          models. If the quadratic term manipulation$^2$ 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 $\pm$ 1000mm (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 (manipulation$^2$) term upon the flight variables can be illustrated by

297    comparing the $R^2$ (proportion of variance explained) of each model with and without the

298    quadratic term (Table 4). The percentage change in $R^2$ caused by the removal of the quadratic

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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

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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 ∩-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 ∩-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

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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

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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**

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435    **References**

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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 $10^{th}$, $25^{th}$, $50^{th}$, $75^{th}$ and

528 $90^{th}$ percentiles with horizontal lines and all data points outside this range.

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| | mean velocity | mean acceleration | 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** | $F_{1,11} = 5.42$* | $F_{1,11} = 4.64$* | $F_{1,10} = 4.64$ | $F_{1,10} = 12.10$** | $F_{1,10} = 8.04$* |
| **manipulation$^2$** | - | - | $F_{1,10} = 4.96$* | $F_{1,10} = 8.89$* | $F_{1,10} = 5.96$* |

**Table I** Results from the simple General Linear Models for each flight variable examined. Effects of streamer addition (manipulation and manipulation$^2$), initial flight variable, site and year are shown. If the quadratic term manipulation$^2$ 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 manipulation$^2$), 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 manipulation$^2$ 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 $R^2$ | 99.29 | 81.50 | 53.17 | 80.67 | 89.23 |
| model excluding (manipulation)$^2$ $R^2$ | 91.82 | 81.50 | 29.93 | 63.47 | 77.12 |
| % reduction in $R^2$ | 7.52 | 0 | 43.70 | 21.31 | 13.58 |
|  | $0.5 > p > 0.25$ |  | $0.05 > p > 0.025$ | $0.1 > p > 0.05$ | $0.2 > p > 0.1$ |

**Table IV**  Effect of the manipulation$^2$ term (quadratic function) on the $R^2$ (variance explained) of the final model. The $R^2$ of the model before and after the removal of the quadratic function are shown along with the percentage reduction in $R^2$ (and the p value for the size of the absolute reduction in $R^2$).
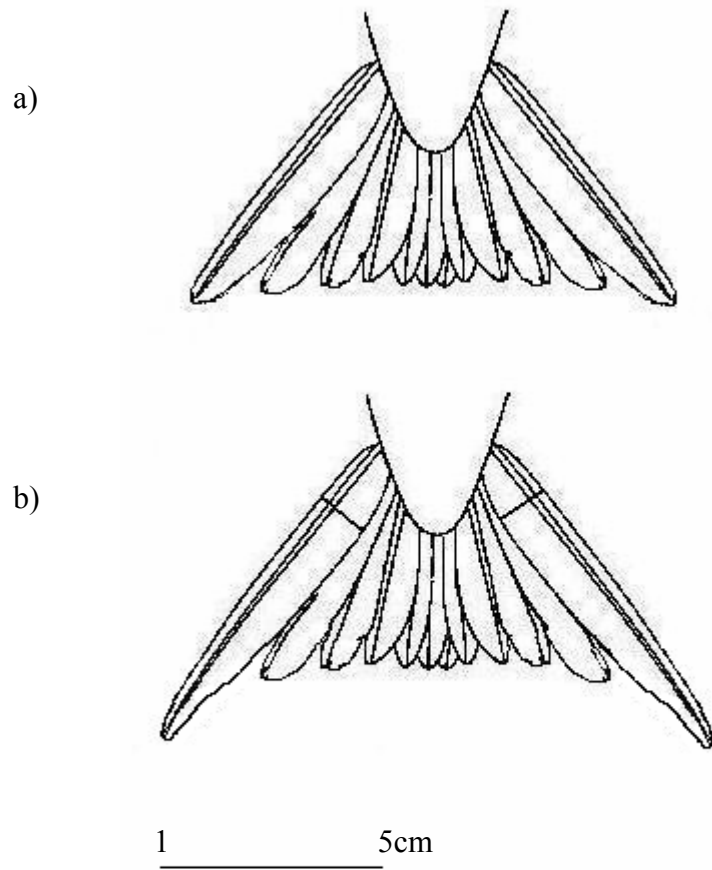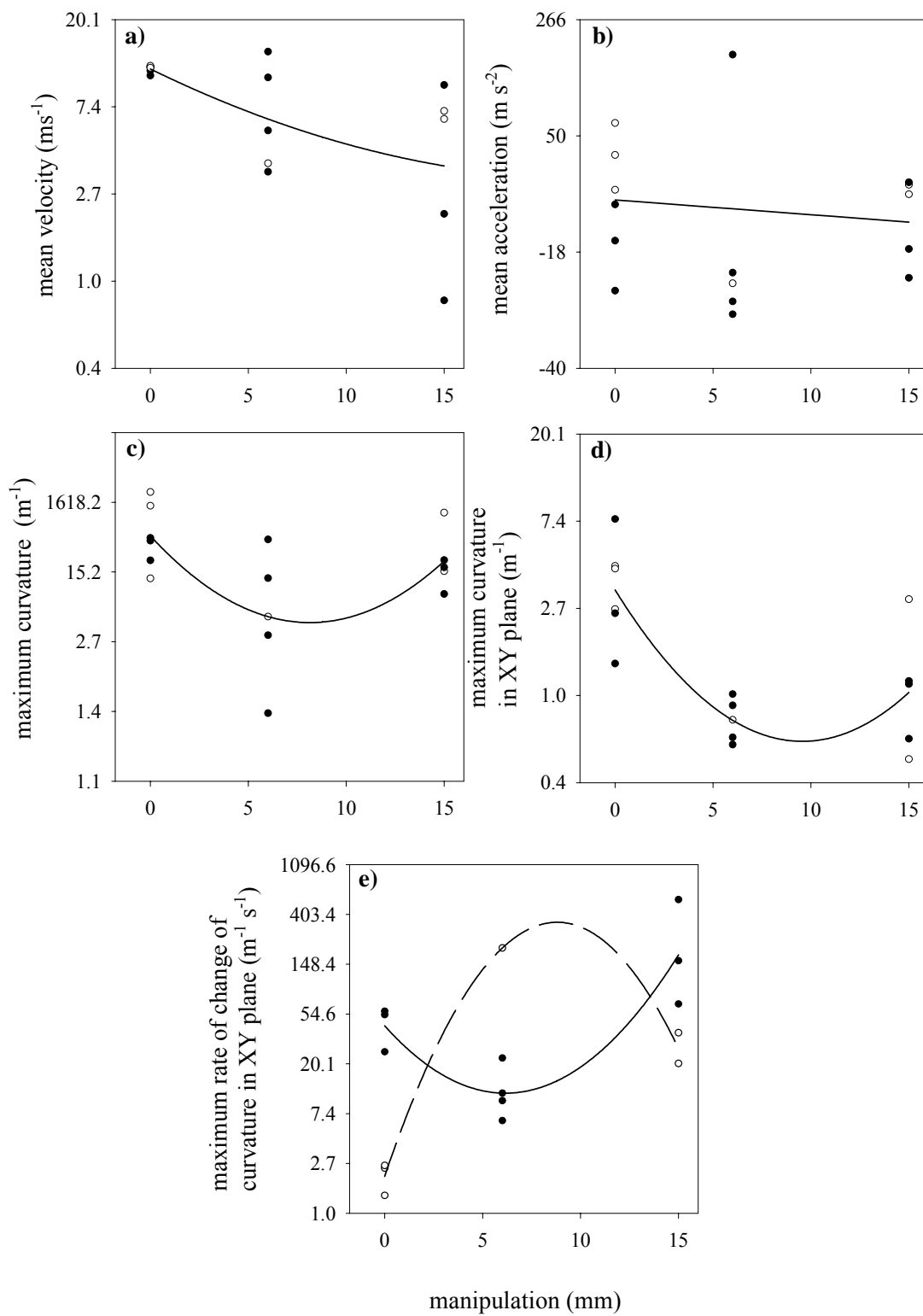
a)

b)

1 _____ 5cm

Fig. 1  Park, Evans and Buchanan

Fig. 2 Park, Evans and Buchanan

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Fig. 3  Park, Evans and Buchanan