Daily energy expenditure of male barn swallows correlates with tail-streamer length: handicap-mediated foraging strategies

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Daily energy expenditure (DEE) of male barn swallows (*Hirundo rustica*), measured using the doubly labelled water technique, correlated with streamer length. Contrary to predictions derived from previous findings, neither a positive linear nor a u-shaped relationship was found between DEE and streamer length. Instead, an n-shaped curve showed that the highest DEE corresponded to an intermediate streamer length of 119 mm. A model incorporating estimates of resting metabolism and flight energy expenditure from aerodynamics models suggested that variation in individual tail dynamics was the most likely explanation for the observed DEE. We suggest that streamer length is coupled to foraging strategy, because tail dynamics control flight performance, which in turn influences flight behaviour.

Keywords: sexual selection; flight; tail streamer; *Hirundo rustica*; energetics; doubly labelled water

1. INTRODUCTION

The hypothesis that exaggeration of male barn swallow (*Hirundo rustica*) streamers confers a suite of mating benefits and is the result of female choice has growing support (Møller 1994). Theoretically, while bestowing mating benefits, streamers should also impart flight costs (Evans & Thomas 1992). Enlargement of tail area increases parasite drag and therefore the power required to overcome it, but because streamers are behind the maximum continuous span of the tail, there is no corresponding contribution to lift (Thomas 1993, but see Norberg 1994). Streamer length-mediated changes in moments of inertia, drag of the tail and overall body mass will also affect agility and manoeuvrability during flight (Evans & Thomas 1992). Several studies have shown tail streamers to be elongated beyond their optimum length for manoeuvrability (Buchanan & Evans 2000; Park *et al.* 2000; Rowe *et al.* 2001). One study investigated whether streamers increase the energetic cost of flight, but no effect

of tail-streamer length manipulations on daily energy expenditure (DEE) was found (Cuervo *et al.* 1996). DEE was taken to be representative of flight energy expenditure (FEE) because the study coincided with nestling rearing when males spent much time in flight foraging for their young. Statistical power associated with the data analyses of Cuervo *et al.* (1996), however, was low. Hence, it is possible that streamer manipulations caused undetected and individual-specific behavioural effects masking any relationship between streamer length and DEE. If a significant aerodynamic cost of streamer length existed, we might expect increased DEE with original streamer length. Accordingly, we used doubly labelled water (DLW; Speakman 1997) to measure the DEE of unmanipulated free-living male barn swallows. We hypothesized that streamer length would positively correlate with DEE since increased aerodynamic drag and sexual selection theory predicts increasing costs (here DEE) with increasing ornament size (here streamer).

2. MATERIAL AND METHODS

Fieldwork took place during 1997 and 1998, in central Scotland (56°8' N, 3°54' W). Swallows discussed here were 18 unmanipulated control-group birds from a larger study (Spencer & Bryant 2002). Birds were caught using mist-nets between 17.00 and 19.30. DLW was used to measure DEE (see electronic Appendix A available on The Royal Society's Publications Web site). After initial body water samples were taken, birds were placed in an outside shelter overnight at ambient temperature. Birds were released at dawn, ensuring a normal foraging period. The overnight period averaged 7.2 ± 0.5 hours.

Experiments were undertaken when chicks were 10–14 days old, when provisioning rates were at their peak. After recapture of adults, chicks were weighed to establish brood mass. Nest visitation rate was measured with a video (25 Hz) between 08.00 and 12.00 for a period of 1.4 ± 0.4 hours. Nest visitation rate, clutch size, fledging age, brood mass and number of chicks fledged provided measures of short-term reproductive success. Data were normally distributed and consequently all statistical tests were parametric, and performed using MINITAB v. 10.5extra. Means are $\pm$ s.e. unless otherwise stated.

To determine whether the relationship between DEE and streamer length reflected FEE, FEE was estimated using the flight model of Pennycuik (1989), with the effects of tails incorporated using the model of Thomas (1996), adjusted as per Evans *et al.* (2002). The model estimate for an individual used each bird's morphological measurements, corresponded to minimum power speed and assumed a daily flight duration of 10 hours (Westerterp & Bryant 1984). A chemical to mechanical energy conversion efficiency of 18% was used (Ward *et al.* 2001). A realistic tail-spread angle of 80° and tail angle of attack of 20° were used as estimates of average tail dynamics during foraging flights (Evans *et al.* 2002).

3. RESULTS

A second-order polynomial regression provided the best fit for the relationship between DEE and tail-streamer length (figure 1). Year (1997–1998) had no effect ($F_{1,14} = 0.68$, $p = 0.423$) and was consequently removed from the final model. The polynomial predicted a tail streamer of 119 mm in length to represent the highest DEE (71.2 kJ d^{-1}). If the data for two males with the longest streamers were removed, however, the relationship between DEE and streamer length was described by a straight line. Streamer length was not a correlate of body mass ($F_{1,16} = 0.37$, $p = 0.553$) or wing length ($F_{1,16} = 2.26$, $p = 0.153$).

Short-term measures of reproductive success did not vary linearly or curvi-linearly with streamer length ($p > 0.3$). Similarly, adult mass loss did not indicate that adult condition deteriorated systematically with streamer length (second-order polynomial, $F_{2,15} = 1.23$, $p = 0.319$; linear regression, $F_{1,16} = 0.87$, $p = 0.364$). There was no

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Figure 1. A second-order polynomial relationship ($F_{2,15} = 4.37$, $r^2 = 0.37$, $p = 0.032$) was found between DEE and tail-streamer length, $y = -730.97 + 13.5x - 0.0568x^2$. Also shown is the line of best fit ($F_{1,14} = 9.7$, $r^2 = 0.41$, $p < 0.001$) when the data for the two swallows with the longest streamers (open circles) were excluded, $y = -45.9 + 1.86x$.

Figure 2. Relationships between estimates of FEE excluding RMR (circles) and streamer length, and estimated DEE (FEE + resting metabolism rate (RMR)) (squares) and streamer length. The curve represents the measured relationship between DEE and streamer length (figure 1). Neither estimated FEE (second-order polynomial, $F_{2,15} = 0.14$, $r^2 = 0.02$, $p = 0.871$; linear regression, $F_{1,16} = 0.21$, $r^2 = 0.01$, $p = 0.656$) nor estimated DEE (second-order polynomial, $F_{2,15} = 0.36$, $r^2 = 0.05$, $p = 0.705$; linear regression, $F_{1,16} = 0.01$, $r^2 = 0.01$, $p = 0.912$) was found to vary predictably with streamer length.

relationship between DEE and visiting rate ($F_{1,16} = 0.03$, $p = 0.865$).

Modelled FEE did not vary in a predictable manner with streamer length (figure 2). Adding an estimate of resting metabolism rate (RMR; see electronic Appendix A) to the estimate of FEE did not change the shape of the relationship between estimated DEE and streamer length. Time spent in flight being equal, estimated energy

Figure 3. Relationships between average tail dynamics and streamer length, if theoretical estimates of DEE were accurately to model measured DEE. (a) The relationship between tail-spread angle and streamer length, $y = -2159 + 37.5x - 0.157x^2$ ($F_{2,15} = 18.9$, $r^2 = 0.68$, $p < 0.001$). (b) The relationship between tail angle of attack and streamer length, $y = -579 + 10.0x - 0.0419x^2$ ($F_{2,15} = 18.25$, $r^2 = 0.67$, $p < 0.001$).

expenditure owing to flight and basal processes did not vary predictably with streamer length (figure 2).

The effect of tail dynamics was examined by determining whether the observed pattern of DEE could be accurately modelled by varying tail dynamics between individuals (figure 3). To reduce estimated FEE, tail angle of attack and tail-spread angle must be reduced to decrease drag. For these calculations, individual morphology measures were used, flight time was held constant for each individual (10 hours) and mean tail angle of attack was maintained at 20° , while the mean tail-spread angle was varied. Then the tail-spread angle was maintained at 80° while the tail angle of attack was varied. Using these criteria, mean tail angle of attack was inferred as $12.4^\circ \pm 0.5$ and mean tail-spread angle as $54.9^\circ \pm 1.0$. Using lines of best fit, second-order polynomials, a swallow with a 120 mm streamer would be predicted to have the most extreme average tail dynamics: a tail-spread angle of 80.2° or a tail angle of attack of 17.64° . Assuming no change in non-flight behaviour or tail dynamics, to model

Table 1. The relationship between life-history components and male barn swallow streamer length.

life-history component (<i>y</i> -axis)	shape of relationship with streamer length (<i>x</i> -axis) 90 mm —————> 135 mm
female provisioning rate–male quality–viability of offspring (Møller 1988, 1994; de Lope & Møller 1993; Møller & de Lope 1994)
prey size–male turning ability (de Lope & Møller 1993; Buchanan & Evans 2000; Rowe <i>et al.</i> 2001)	
DEE–tail dynamics (angle of attack and spread angle)

the measured DEE the time spent in flight by swallows in this study would be predicted to range unrealistically between 3.9 and 9.0 hours.

4. DISCUSSION

The hypothesis that DEE would increase progressively with streamer length was not supported here. Instead, DEE peaked at a streamer length of 119 mm then declined. The relationship was dependent upon the two males with the longest streamers, but there was no valid reason for removing them from the dataset. The polynomial relationship was not consistent with modelled estimates of DEE derived by combining RMR and FEE. Neither is the relationship between DEE and streamer length found here consistent with classic studies of sexual selection in the swallow that suggested increasing costs with increasing streamer length (Møller 1994). Additionally, the relationship between cost (DEE) and trait (streamer) is the inverse of what would be predicted by more recent work, which implicates a combination of natural and sexual selection in the evolution of swallow streamers (Buchanan & Evans 2000; Rowe *et al.* 2001). It therefore appears that DEE is not a measure of overall male ‘fitness’. We suggest instead that DEE reflects differential foraging strategies.

According to flight models (Pennycuick 1989; Thomas 1996), observed variation in streamer lengths would not, in an all-other-things-being-equal scenario (i.e. time in flight and tail dynamics), produce a large increase in FEE (less than 0.5%). Furthermore, such small increases in FEE could not be detected using DLW (Speakman 1997). By contrast, large variations in DEE can be produced by subtle changes in average tail dynamics. When realistically maintaining time spent in flight as a constant variable across individuals (Westerterp & Bryant 1984) and varying either tail-spread angle or angle of attack, the observed pattern of DEE variation with streamer length can be modelled. Moreover, the range of estimates of average tail

dynamics seen in our model (figure 3) appear realistic (Evans *et al.* 2002). The same results could be achieved by varying the tail-spread angle and angle of attack simultaneously, but although perhaps more realistic, such an analysis would be unnecessarily complicated.

Why might we expect tail dynamics to vary between individual swallows? Previous work has shown that the effects of streamer-length manipulations are different depending upon original length (Buchanan & Evans 2000). Because flight costs are not solely dependent upon streamer length, and individual morphologies are highly variable, there are likely to be subtle differences in the optimum flight strategies of individual swallows, with some individuals better adapted, for example, for speed or agility (Buchanan & Evans 2000). If this applies, individuals may change their foraging strategy depending upon their flight capability. Swallows appear to prefer large Dipteran prey over smaller ones and large Diptera are strong flyers capable of actively avoiding capture (Turner 1982). Swallows with better turning ability may be able to catch large Diptera, whereas those lacking agility may benefit from taking less profitable but less evasive prey. Such within-population differences in foraging strategies are widespread. There are at least 93 animal species where sympatric ecologically differentiated individuals have been detailed, and 18 bird species contained within the list exhibit sympatric divergence in foraging strategies (Bolnick *et al.* 2003).

If foraging strategy varied with streamer length we might expect adult condition or reproductive success to be affected, but this was not the case here. Statistical powers associated with analyses of measures of reproductive success, however, were low ($1 - \beta < 0.35$) and therefore any interpretations should be treated with caution.

Combining our findings with previously observed relationships between life-history variables and male streamer length (table 1) allows predictions about male swallow optimum foraging strategies to be made. To achieve

a given turn radius, long-streamered males require more extreme tail dynamics or long streamers may inhibit tight turns: Rowe *et al.* (2001) demonstrated that streamer length influences turning ability in swallows. Therefore, they expend less energy taking less profitable prey (small diptera) because it requires little deviation from the flight path. To compensate for reduced male foraging efficiency, females paired with long-streamered males increase their chick provisioning rates as shown by de Lope & Møller (1993). Females are prepared to increase their own provisioning rates because the possession of long streamers advertises male quality: increased offspring viability, reproductive success and survival rates, and decreased susceptibility to parasitism (Møller 1988, 1994; de Lope & Møller 1993; Møller & de Lope 1994). Males with 119–120 mm streamers capture large profitable prey and perhaps some smaller prey and their DEE is high, owing to the power demands required to perform turns when capturing profitable large Diptera. Males with shorter streamers catch more profitable prey than males with long streamers (Møller 1988), because turning ability is best at shorter streamer lengths (Møller 1994) and their morphology allows tight turns to be performed with less extreme tail dynamics and consequently at lower power levels.

Our conclusions are contrary to the 'Norberg effect', which predicts increasing lift enhancement with streamer length (Norberg 1994). The most realistic hypothesis for the results presented here, however, appears to be a change of foraging strategy with streamer length. Optimum behaviour may differ between individuals and therefore the new optimum behavioural strategy, after a given change in handicap, will also differ. Consequently, interpretation of the shape of the relationship between a single-cost variable and handicap size (Buchanan & Evans 2000), for across individual datasets, may not be suitable for hypothesizing about selective pressures responsible for trait evolution. To test our predictions, stereo video (Buchanan & Evans 2000) can be used to film male barn swallows during foraging flights and turning performance related to tail dynamics, and streamer length. In addition, prey items brought to the nest can be recorded using chick bolusing or adult regurgitation techniques. It would be interesting to determine whether foraging strategy is fixed to original streamer length or plastic and alterable by manipulating streamer length. In addition, could attachment of streamers to house martins, that do not naturally possess tail streamers, induce a change in foraging strategy as well as a change in manoeuvrability (Park *et al.* 2000)?

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