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Energetic cost of tail streamers in the barn swallow (*Hirundo rustica*)

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Abstract Different hypotheses stress the importance of natural or sexual selection to explain the evolution and maintenance of long outermost tail feathers in the barn swallow (*Hirundo rustica*). Since energy costs are predicted to arise from tail length manipulation, we measured the daily energy expenditure in three experimental groups (tail-shortened, tail-elongated, and control birds) with the doubly labelled water technique. Though we did not directly measure flight cost, we assumed this to be positively related to daily energy expenditure. Mass independent daily energy expenditure ($\text{kJ}/\text{mass}^{0.67}$ day), average daily metabolic rate ($\text{ml CO}_2/\text{g h}$), and water flux ($\text{ml H}_2\text{O}/\text{g day}$) did not show any significant difference among treatments in either sex. Males had higher values than females for the three parameters. Males with short original tail length experienced a higher water flux than originally long-tailed males. Females that laid more eggs during the breeding season or had heavier broods also showed higher levels of water flux which could imply a higher food intake. Our expectation of finding energetic costs of manipulated tail length in barn swallows with an integrated measure of metabolism was not fulfilled, and we did not find evidence for behavioural changes in the birds involved in the experiment.

Key words Doubly labelled water · Energy expenditure · Metabolism · Sexual selection · Tail ornament

Introduction

In many bird species males have exaggeratedly long tails compared to those of females. Some experimental studies have shown that females prefer to mate with long-tailed males: *Euplectes progne* (Andersson 1982), *Hirundo rustica* (Møller 1988), *E. jacksoni* (Andersson 1992), and *Nectarinia johnstoni* (Evans and Hatchwell 1992). This means that the tail in these species is a secondary sexual character, an ornament maintained by female choice. Whatever model of sexual selection is considered, they always assume that exaggerated long tails will be costly to produce and maintain. The cost of the tail can be balanced by the benefits males achieve in terms of mating success (Fisher 1930; Lande 1981; O'Donald 1980; Pomiankowski et al. 1991), or the cost may be a necessary condition in a honest signalling system, reflecting inherent differences in phenotypic or genetic quality among males (Grafen 1990a,b; Hamilton and Zuk 1982; Iwasa et al. 1991; Zahavi 1975, 1977).

Although in this study we have only considered energetic costs, hypothesized maintenance costs of long tails include increased risks of predation and parasitism (review in Magnhagen 1991). Increased flight costs associated with extravagant feather ornamentation in birds are mainly due to the induced drag caused by the presence of long, unwieldy feathers (Evans and Thomas 1992). Also turning ability is dependent to a large extent on tail length. The ability to turn quickly and to maintain control under adverse conditions is essential in prey capture and in avoiding crashes and predators (Cuthill and Guilford 1990). In addition, the immunocompetence hypothesis (Folstad and Karter 1992) predicts that testosterone will enhance the expression of male sexual characters (i.e. long tails) while exerting a

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suppressive effect on the immune system thereby exposing hosts to higher intensities of parasite infestations.

In the species we have chosen as the subject of our study, the barn swallow (*Hirundo rustica*), two experimental studies have shown that the possession of a long tail by the males results in a cost in terms of viability (Møller 1989; Møller and de Lope 1994). Males with experimentally elongated tail ornaments captured smaller, less profitable prey than those with shortened tails. They also decreased their natural tail size during moult, causing a fitness loss resulting from reduced sexual attractiveness during the following year. Another assumption of the handicap principle explaining the evolution of reliable signalling is that cheating is prevented because the cost of a signal is greater for low-quality than for high-quality individuals (Zahavi 1975; Andersson 1986; Grafen 1990a; Heywood 1989; Iwasa et al. 1991; Møller 1991). Møller and de Lope (1994) found that naturally long-tailed males were better able to survive with an elongated tail, whereas naturally short-tailed males improved their survival following tail shortening, supporting the assumption of a differential cost of the signal.

Although tails can be used as signals, the most obvious function of bird tails is aerodynamic (Pennycuik 1968, 1975; Thomas 1993). There are some suggestions that the elongated tails of the barn swallow are aerodynamically functional (Balmford et al. 1993; Norberg 1994; Pennycuik 1975; Thomas 1993). The streamers (the outermost tail feathers) improve manoeuvrability by allowing tighter turns, and, as a consequence, increasing the number of insects the swallow can capture per unit time (Norberg 1994). But even if long tail streamers may give rise to natural selection advantages due to the effects on manoeuvrability or general flight performance, this hypothesis obviously has its limitations because it cannot explain sexual size dimorphism in barn swallow tail length.

An indirect way of calculating cost of flight is by measuring energy expenditure. We used the doubly labelled water technique, successfully used before with several species of Hirundinidae (Hails and Bryant 1979; Turner 1980; Westerterp and Bryant 1984). With this method we are assessing an integrated measure of energy cost of all activities averaged over a long period of time (one day in our case). Variation in daily energy expenditure may show variation in cost of flight if all the individuals spend the same time flying and distribute their time among activities in the same way. This assumption could be not far from reality in our study, since experiments were carried out when chick food demand reached a peak (9–15 days old) and adults spent all daylight hours catching insects to feed their always hungry chicks.

For a better understanding of the function of the long outermost tail feathers in the barn swallow we manipulated their length and determined energy expenditure of these individuals. If sexual selection is the most important process governing elongation of outer-

most tail feathers, birds will bear tails longer than the optimum according to natural selection. In this case we would expect individuals with artificially elongated tails to expend more energy than non-manipulated birds, and artificial tail shortening would give rise to lower energy expenditure rates. On the other hand, if natural selection has the major influence on tail length, we would expect birds both with elongated and shortened tails displaced from the optimal tail length under natural selection to expend more energy than non-manipulated ones.

Methods

The barn swallow is a small (about 20 g) insectivorous passerine that feeds on the wing and usually nests in small colonies. Sexual size dimorphism is slight with the exception of the outermost tail feathers, which are longer in males than in females, and longer in females than in juveniles of either sex (Cramp 1985; Møller 1994). The experiments were performed at Badajoz, Spain, during the breeding seasons of 1992–1994. The study area consists of open farmland with scattered groups of trees around farms and rivers (de Lope 1983).

In 1992 and 1993 birds were caught in mist nets when their chicks (first brood) were 9–15 days old and their outermost tail feathers were manipulated. In 1994 tail feathers were manipulated when birds arrived at the breeding grounds (February and early March) from their West African winter quarters, around one month before the start of laying of the first clutch. Several morphological measurements were also taken and each bird was provided with a metal ring and a combination of colour plastic rings.

Barn swallows were randomly assigned to three experimental groups: (i) shortening, in which the two outermost tail feathers were reduced in length by 20 mm; (ii) elongation, in which the two outermost tail feathers were cut and a 20-mm piece was added; and (iii) a control group in which tail length was not manipulated. The first group (shortened) had a 20-mm-long piece of feather cut 10 mm from the base of each of the two outermost tail feathers. The apical part of the feathers was glued back on the original feather using cyanoacrylate superglue. The second group (elongated) had also the outermost tail feathers cut 10 mm from the base and then the 20-mm-long piece of feather from the shortened group glued between the basal and the apical pieces. Tail feathers were cut and glued near the base where feathers have their maximum width (Møller et al. 1995b). The third group of birds (control) was captured, measured and ringed, as birds in the other two groups, but their tail feathers were not manipulated. We did not include a second control group, with feathers cut and glued again to control for treatment effects, since previous experiments have shown that treatment itself had no effect (Møller 1988, 1992).

Daily energy expenditure in the three treatments was measured using the doubly labelled water technique, first described by Lifson and McClinton (1966), and reviewed by Nagy (1980), Speakman and Racey (1988), and Bryant (1989). All birds involved in the experiment were caught when their chicks (first brood) were 9–15 days old (when nestling growth peaks and feeding rates reach a maximum), weighed with a Pesola spring balance to the nearest 0.25 g and injected intraperitoneally with 0.1 ml of a mixture containing 7.23 g of 90.43 AP H₂¹⁸O and 3.67 g of 99.9 AP D₂O. After the birds had spent one hour in a cage for equilibration of the injected water in the body fluids, blood was sampled from a brachial vein, collected in flame-sealed heparinized capillary tubes and stored until analysis at the Centre for Isotope Research (CIO) of the University of Groningen, Netherlands. Approximately 24 h after the first blood sampling, the birds were caught again, weighed, and a second set of blood samples collected from the vein in the opposite wing to that used for the first sample. We also recorded, for each bird, feeding rates during 1-h observation periods between

1400 and 1900 hours (the day between the two blood samplings). In all cases experiments were carried out in similar weather conditions (i.e. sunny, calm days) to avoid variation in insect or bird behaviour (Elkins 1995; Taylor 1963; Wigglesworth 1972).

In 1992 and 1993 swallows (20 males and 3 females) were caught during the morning, immediately injected, and blood samples collected one hour later. They were caught again the next day just a few minutes before second blood samples should be extracted. In 1994 the 13 males and 35 females involved in the experiment were caught before dawn and then injected and their blood collected during the morning. After blood sampling they were released, but some individuals were kept in cages longer than others. They were caught the next day also at dawn and kept in cages until 24 h after the first blood sampling.

To calculate daily CO_2 production from fractional turnovers of the two isotopes we have used the equations by Lifson and McClintock (1966) and Nagy (1980). From these we have derived average daily metabolic rate (ADMR, in $\text{ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$). To assess body water pools we used the equation derived by Westerterp and Bryant (1984) $\text{H}_2\text{O (ml)} = 0.325 \text{ mass (g)} + 5.06$. CO_2 production is related to O_2 consumption through the respiratory quotient (RQ), which depends on the diet. We used the energy equivalent for CO_2 from an insectivorous diet (RQ = 0.75). Daily energy expenditure (DEE) was derived from O_2 consumption by assuming that every litre of oxygen consumed in metabolism produces 4.8 kcal or 20 kJ independently of the oxidized substratum (Weathers and Sullivan 1989). Metabolic rate has an allometric relationship with body mass. Therefore to adjust for the effect of body mass on metabolism, we divided DEE by $\text{mass}^{0.67}$ (Heusner 1985, Williams 1988), obtaining the mass-independent daily energy expenditure (MIDEE, in $\text{kJ/mass}^{0.67} \text{ day}$). The DLW technique also allows us to evaluate food consumption through water flux ($\text{ml H}_2\text{O/day}$) assuming that all water ingested comes from the food.

Statistical analyses were performed according to Siegel and Castellan (1988) and Sokal and Rohlf (1981). We tested whether response variables were normally distributed (Lilliefors tests) before analyses of variance (ANOVA) and covariance (ANCOVA). Percentage of feedings was arcsin-transformed before analyses, in order to obtain an approximately normal distribution. Pearson correlation coefficients were Bonferroni corrected. For some tests we performed statistical power analysis according to Cohen (1988). Statistical tests used are two-tailed. Values are means (SE).

Results

We did not find any significant difference among years for morphological characters (original tail length, mass), brood characteristics (brood mass, brood size), and parenting performance (percentage of feedings) for the male swallows involved in the experiment (one-way ANOVAs, $0.18 \leq F \leq 2.90$, $df = 2, 30$, $0.07 \leq P \leq 0.83$). MIDEE, ADMR and water flux per unit body mass did not differ significantly among years either (one-way ANOVAs, $0.014 \leq F \leq 0.78$, $df = 2, 30$, $0.47 \leq P \leq 0.99$). In view of these results, we pooled the data from the three years for subsequent analyses. We did not investigate differences for females among years since almost all of them (35 out of 38) were manipulated in 1994.

The 33 male and 38 female barn swallows in our study expired on average 8.21 (0.18) and 7.92 (0.17) $\text{ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$, respectively, which amounts to a DEE of 90.19 (2.25) and 85.13 (1.93) kJ/day , and to a MIDEE of 13.12 (0.29) and 12.58 (0.27) $\text{kJ/mass}^{0.67} \text{ day}$. These values are 10–11% lower than the values for Scottish swallows reported by Westerterp and Bryant

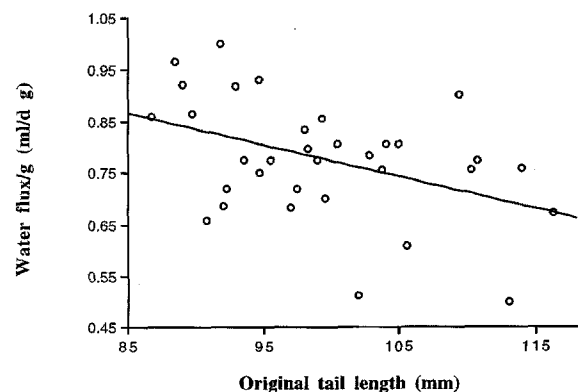
(1984). Water flux per unit mass was 0.78 (0.02) (males) and 0.71 (0.02) (females) $\text{ml H}_2\text{O g}^{-1} \text{ day}^{-1}$.

If tail length affects the costs of flight, we could expect an effect of treatment on energy expenditure or metabolic rate. We tested this prediction by comparing experimental groups using ANCOVAs with treatment as a factor. We used as covariates some of the variables we believed could affect metabolic rate: original tail length, brood mass, time spent in the cages (an artefact due to experimental methods in 1994), and the interaction between treatment and original tail length. No significant differences among experimental treatments were found for MIDEE, ADMR and water flux per unit mass in either sex (ANCOVAs, $0.04 \leq F \leq 1.23$, $n = 33$ in males, $n = 38$ in females, $0.30 \leq P \leq 0.96$). We also checked the power of these ANCOVA tests (Cohen 1988) and found it in all six cases (MIDEE, ADMR, and water flux in males and females) to be lower than 0.06 (power analysis, power < 0.06 , $0.004 \leq f \leq 0.021$, $\alpha = 0.05$, $u = 2$, $n = 11$ in males, $n = 12.7$ in females).

The only variable that showed a significant relationship with male metabolic parameters was original tail length (ANCOVA, $F = 11.4$, $n = 33$, $P = 0.002$). Males with short original tails experienced more water flux per unit body mass than originally long-tailed males (Fig. 1). This result could mean that they consumed more food without resulting in an increase in metabolic rate or energy expenditure. A difference in food intake should predict a differential weight variation in originally long-tailed males compared to short-tailed ones. However, original tail length, although showing the expected trend, is not significantly correlated with relative variation in weight [$(\text{weight}_{2\text{nd blood sampling}} - \text{weight}_{1\text{st blood sampling}}) / \text{mean weight}$] after controlling for treatment (Kendall partial rank-order correlation coefficient, partial tau = -0.13 , $n = 22$, $P = 0.40$).

In the case of females, brood mass showed a significant influence on water flux (ANCOVA, $F = 4.29$,

Fig. 1 Water flux per unit mass in relation to the original tail length of male barn swallows. Pearson correlation coefficient, $r = -0.42$, $n = 33$, $P = 0.014$. The line is the model I linear regression line ($y = 1.39 - 0.0062x$)



$n = 38$, $P = 0.047$). Females with heavier broods had higher levels of water flux per unit mass after controlling for treatment and time spent in the cages (Kendall partial rank-order correlation coefficient, partial $\tau = 0.24$, $n = 38$, $P = 0.035$).

To estimate the differences between sexes, we included sex as a factor in the ANCOVA model previously used, year (most females were captured in the same year while males were captured during three years), and the interaction between treatment and sex. The tests show significant differences between sexes for MIDEE, ADMR, and water flux (ANCOVAs, $6.94 \leq F \leq 8.48$, $n = 71$, $0.005 \leq P \leq 0.011$). Figure 2 shows that males have higher values than females for the three parameters.

If birds with experimentally elongated tails did not expend more energy than short-tailed individuals, and assuming that tail length affects the cost of flight, this apparent paradox could be explained if they spent more time flying in a less energy-consuming gliding flight. If that was the case, foraging efficiency of long-tailed individuals should have deteriorated and they would have fed their young less often or with smaller prey. As a consequence, their chicks should have increased in weight less than those of short-tailed individuals. First, we found no significant differences in number of feedings among the three experimental groups in either sex after controlling for the effects of original tail length and brood mass (ANCOVAs; females: $F = 1.06$, $n = 38$, $P = 0.31$; males: $F = 0.02$, $n = 33$, $P = 0.89$). Only the brood mass significantly influenced the number of feedings in both sexes (ANCOVAs; females: $F = 5.81$, $n = 38$, $P = 0.022$; males: $F = 17.6$, $n = 33$, $P < 0.001$) (Fig. 3). The number of feedings was not significantly correlated either with MIDEE or original tail length after controlling for treatment in either sex (Kendall partial rank-order correlation coefficient, $-0.11 \leq \text{partial } \tau \leq 0.15$, $n = 33$ in

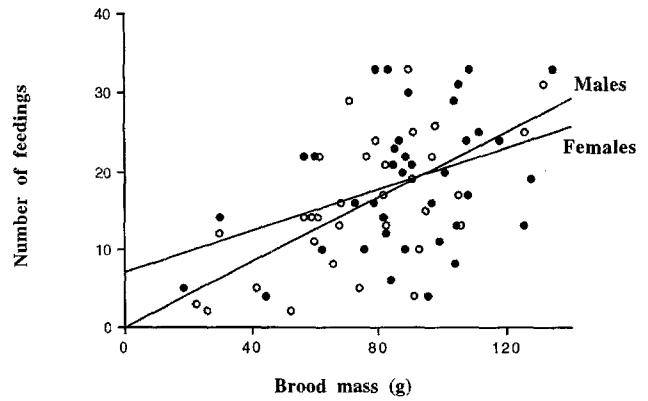
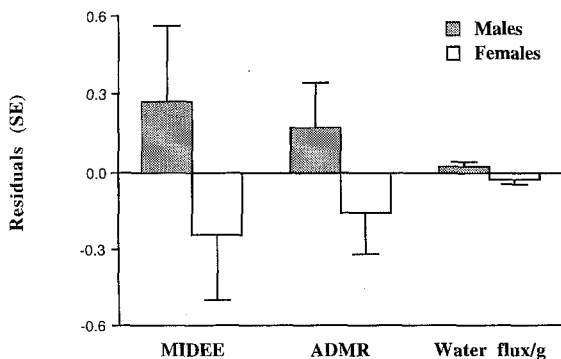


Fig. 3 Number of feedings to the young in relation to brood mass. Males (open circles), Pearson correlation coefficient, $r = 0.62$, $n = 33$, $P < 0.001$. Females (solid circles), $r = 0.38$, $n = 38$, $P = 0.018$. The lines are the model I linear regression lines (males: $y = -0.14 + 0.21x$; females: $y = 6.83 + 0.13x$)

males, $n = 38$ in females, $0.23 \leq P \leq 0.76$). Regarding brood mass variation (brood mass_{2nd blood sampling} – brood mass_{1st blood sampling}), we did not find any difference among treatments for either sex after controlling for original tail length, brood mass and brood age (ANCOVAs; females: $F = 1.32$, $n = 35$, $P = 0.28$; males: $F = 0.42$, $n = 13$, $P = 0.67$). Brood age influenced brood mass variation in the expected direction: older broods increased less in mass than younger ones (Kendall rank-order correlation coefficient; females: $\tau = -0.45$, $n = 35$, $P < 0.01$; males: $\tau = -0.72$, $n = 13$, $P < 0.01$). Another possibility would be that mates compensated when one individual decreased its feeding frequency. However, we did not find any difference in percentage of feedings to the young among treatments for either sex (ANCOVAs; females: $F = 0.15$, $n = 38$, $P = 86$; males: $F = 1.07$, $n = 32$, $P = 0.36$). Brood mass affected the percentage of feedings, but only in the case of males (Fig. 4).

Fig. 2 Mass independent daily energy expenditure (MIDEE in $\text{kJ}/\text{mass}^{0.67} \text{ day}$), average daily metabolic rate (ADMR in $\text{ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) and water flux g^{-1} (in $\text{ml H}_2\text{O g}^{-1} \text{ day}^{-1}$) of male ($n = 33$) and female ($n = 38$) barn swallows. Values are residuals from ANCOVAs using treatment and year as factors and original tail length, time spent in a cage, brood mass, interaction between treatment and original tail length, and interaction between treatment and sex, as covariates



Discussion

The most important finding of this study was that we did not find any difference in energy expenditure (MIDEE) or metabolic rate (ADMR) among treatments. That is to say, experimental manipulation of swallow tail length did not affect any of the energetic parameters. Assuming a relationship between energy expenditure during the experimental period (24 h) and cost of flight, we can think of two possible explanations for this result: (i) either tail streamers do not have any effect on the cost of flight, or, (ii) if they do, birds with different treatments were flying for different lengths of time or in different ways. Let us first consider the second possibility. The first consequence would be some variation in the number of feedings to the young and/or in prey size among treatments. Swallows feed mainly on dipteran prey during the breeding season, preferring large prey items over small

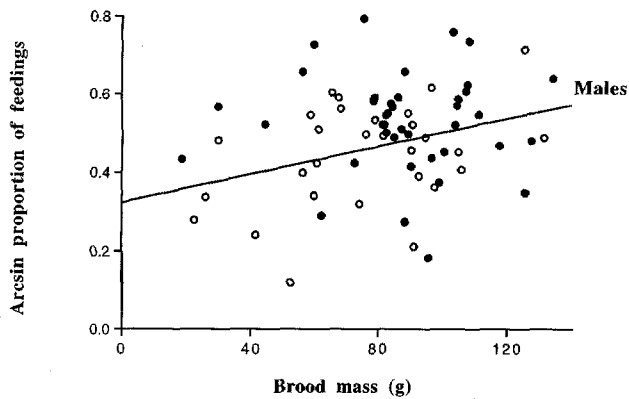


Fig. 4 Arcsin of proportion of feedings to the young in relation to brood mass. Males (*open circles*), Pearson correlation coefficient, $r = 0.37$, $n = 32$, $P = 0.037$. Females (*solid circles*), $r = 0.001$, $n = 38$, $P = 0.99$. The *line* is the model I linear regression line (males: $y = 0.32 + 0.0018x$)

ones (Turner 1980, 1982). Large diptera are strong flyers which can actively evade capture attempts by swallows (Waugh 1978). In our study we did not measure prey size, but in other studies of the barn swallow it has been shown that size of prey captured by male barn swallows decreased with experimental tail length (Møller and de Lope 1994; Møller et al. 1995a), or, at least males with elongated tails brought significantly smaller prey items than males with shortened or non-manipulated tails (Møller 1989). Two mechanisms could explain the change in composition of boluses brought to offspring: males may have switched foraging mode and spent more time in less expensive gliding flight, or they may have switched foraging habitat.

For the number of feedings to the young we found no differences among groups. This result does not suggest that birds from the three experimental groups flew in different ways. Only brood mass correlated with number of feedings which seems obvious. Heavier broods, which mainly means broods with more chicks, required larger amounts of food which was supplied by both sexes (Fig. 3). Regarding the possibility that some birds fed their young with larger prey items than others, this could result in variation in brood mass since net energy gain is higher by catching large insects (Turner 1982). Chicks fed large insects should grow faster and/or become heavier. However, our study did not show any difference in brood mass variation among treatments, even after controlling for brood age effects. Brood age is very important for an understanding of brood mass variation because swallow nestlings reach a peak mass on the 14th day after the last young has hatched and then decline until the nestlings fledge (Turner 1980). Our experiments were carried out when most chicks were between 9 and 15 days old, and that is why older broods experienced a smaller increase in mass.

Still there is another possible explanation for the results. Males could compensate when their partners

decreased their contribution in feeding chicks. This has been shown in previous studies on barn swallows (de Lope and Møller 1993; Saino and Møller 1995). De Lope and Møller (1993) showed that foraging efficiency of male barn swallows was negatively related to experimental tail length, and feeding rates of female barn swallows showed a steadily increasing trend from those mated to males with shortened tails to controls to those mated to males with elongated tails. Our experiment, however, does not show this trend. We did not find significant differences in the proportion of feedings among treatments for either sex. Only the brood mass explained a significant proportion of the variation, but only in males: heavier broods were fed more often by the male than by the female (Fig. 4). The result is not very conclusive because we did not find the expected trend for females: females did not feed their young proportionately less when the broods were heavier (Fig. 4). In other species of birds it has been found that whereas males increase their feeding rates in response to brood enlargements, females do not show any change in response to increased brood demand (Moreno et al. 1995; Pärt et al. 1992; Whittingham 1989; Wright and Cuthill 1989).

In addition to these main results we also found interesting relationships between water flux and tail length in males. Water flux was inversely related to original tail length in males (Fig. 1), but no difference in energy expenditure was found. That is to say, males with original short tails may have been eating more, but without increasing metabolic rates or mass more than males with original long tails. Our results suggest that males with long original tails need less food to obtain the same amount of energy. All the results concerning water flux must be taken with reservations since we cannot be sure that there was not a differential water consumption among experimental groups. However, direct water intake was probably unimportant because many of the birds were breeding far away from a suitable drinking place.

Females showed higher water flux (probable food consumption) when they had heavier broods or had laid more eggs during the breeding season, but again without increasing metabolic rates. Females invest more than males in reproduction (they lay and incubate the eggs besides sharing nest building and chick feeding). Probably an important proportion of their energy incomes are invested in compensating egg formation, and larger clutch size increases energy (food) requirements. Since experiments were carried out when chicks were about 2 weeks old this may mean that females still were recovering from egg laying and incubation efforts. Nevertheless, males showed higher levels of energy expenditure, metabolic rate and food consumption than females, even when taking mass differences into account (Fig. 2). This difference in energy expenditure between sexes has already been reported for the barn swallow (Westerterp and Bryant 1984). However, this is not the normal trend

in passerine birds since in most species (10 of 13 species) females spend more energy than males (J. Sanz, unpublished work).

Our expectation of finding energetic costs of tail length manipulation of barn swallows on a daily basis was not fulfilled. Both natural and sexual selection hypotheses for the origin and maintenance of tail streamers predicted some influence of tail streamers in flight performance and so in energetic costs. We did not find evidence of behavioural changes due to the experiment. Therefore, our study does not support either of the two explanations. Furthermore, due to the low power of the statistical tests (see Cohen 1988) comparing the energetic parameters among treatments, we cannot accept the null hypothesis that energy expenditure is unrelated to tail length manipulation. We cannot say that the outermost tail feathers in the barn swallow have no implications for the energetic cost of flight. The effect size in these tests (index of degree of departure from the null hypothesis, calculated in terms of standardized differences among means; see Cohen 1988 for more details) is also very low, and it has a biological implication: tail length variation has at most a small effect on the energetic variables considered. However, other costs of long tails in terms of predation or parasitism may prevent further exaggeration of this secondary sexual character.

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