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Experimental tail elongation in male Barn Swallows *Hirundo rustica* reduces provisioning of young, but only in second broods

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At the beginning of the breeding season, the outermost tail feathers of 31 male Barn Swallows *Hirundo rustica* were either shortened by 20 mm, elongated by 20 mm or left unmanipulated. In first broods, the number of feeding bouts (per nestling per hour) by males and females did not differ significantly among experimental groups. However, in second broods, males with elongated tails fed their nestlings less often than males with shortened or unmanipulated tails. Male tail elongation may have been detrimental to flight, making capture of insects more difficult. Females paired to long-tailed males did not compensate for this reduction in feeding by males and their nestlings received less food. Neither feeding rates nor brood size differed significantly between first and second broods. Variation in abundance of large insects at different times of the day (high around noon and low in the morning and afternoon) matched variation in feeding rates, supporting the importance of large insects in the Barn Swallow diet. Different feeding rate patterns in first and second broods by males with elongated tails could have at least three explanations: (1) such males were able to adjust their parental effort to some extent, temporarily compensating for an imposed handicap; (2) they were more sensitive than males in the other experimental groups to late season food shortage (a decrease in numbers of large insects, the main Barn Swallow prey, was observed as the season progressed); and (3) they were more sensitive than males in the other experimental groups to the deterioration in their physical condition after first broods.

All theoretical frameworks explaining the evolution of secondary sexual characters and mate preferences predict that such characters will be costly at the point of stable equilibrium (Fisher 1930, Zahavi 1975, Iwasa *et al.* 1991, Pomiankowski *et al.* 1991). This cost might be expressed, for example, in terms of increased predation risk or parasitism (Magnhagen 1991, Folstad & Karter 1992). One kind of secondary sexual character is exaggeratedly long tail feathers in males of some bird species (M. Andersson 1982, S. Andersson 1992, Evans & Hatchwell 1992). Long, unwieldy tail feathers cause deterioration in flight performance, mainly due to induced drag and impaired turning ability (Evans & Thomas 1992). According to aerodynamic models (Thomas 1993, 1996, Thomas & Balmford 1995), drag produced by the tail in a flying bird is proportional to tail area, but lift only depends on maximum continuous span. This means that a triangular tail would provide the optimal lift/drag ratio, and any portion of the tail extending beyond that triangle (e.g. very long streamers) would increase drag but not lift. A triangular tail when open (spread) corresponds to a forked tail when closed, with external feathers about twice the length of inner feathers. The less lift there is in relation to drag, the more effort is required to fly, thereby increasing the cost in energy. Lift generated by the tail is particularly important in slow flight and during manoeuvres. Moreover, the tail helps to maintain stability and to control the wing angle of attack, facilitating changes in flight speed. The relative importance of different tail functions determines optimal tail size and shape (e.g. graduated, 'pin-tail', forked) in birds (Balmford *et al.* 1993).

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Male Barn Swallows *Hirundo rustica* have a deeply forked tail, with long outermost tail feathers (longer than in females). Evidence for a sexual function of these feathers has been accumulating over recent years (reviews in Møller 1994, Møller *et al.* 1998). Long-tailed males are preferred by females as mates and extra-pair copulation partners (Møller 1988a). However, an aerodynamic function has also been proposed: that tail streamers work as a control, automatically adjusting the leading edge of the outermost tail feathers when the tail is lowered, causing an increase in the lift/drag ratio in tight manoeuvres (Norberg 1994). Although the function of long tails in Barn Swallows has been the subject of controversy (e.g. Evans & Thomas 1997, Evans 1998, Barbosa & Møller 1999, Hedenström & Møller 1999), it is generally agreed that sexual selection provides at least a partial explanation for tail length in male Barn Swallows (Buchanan & Evans 2000, Rowe *et al.* 2001).

Barn Swallows are aerial insectivores, feeding mainly on flying Diptera and Hymenoptera. This type of food can explain the extraordinary importance of morphological characters related to flight in this species. In the last two decades, various studies have investigated the function of the outermost tail feathers in male Barn Swallows by experimentally manipulating their length. Any modification in aerodynamic cost was predicted to have consequences for foraging efficiency. One study on tail length manipulation and provisioning of young found that males with experimentally elongated tails fed their nestlings less often than males with shortened tails (de Lope & Møller 1993). However, in that study, nestlings of males with elongated tails did not receive less food, as females compensated for the male reduction in food provisioning. De Lope and Møller (1993) suggested that their results support the differential allocation hypothesis (Burley 1986), because females invested more in parental care when mated to more attractive males, but other researchers have suggested that the results could be explained by simple compensation (Witte 1995, but see Møller & de Lope 1995). Another study in a different population of Barn Swallows did not find a significant relationship between male tail length and feeding rates (Møller 1989). Regarding tail length manipulation and prey size, a number of studies have found that males with experimentally elongated tails catch smaller insects than males with shortened or unmanipulated tails (Møller 1989, de Lope & Møller 1993, Møller & de Lope 1994, Møller *et al.* 1995). Catching large insects is energetically more profitable than catching small ones (Turner 1982), but large insects are faster fliers, and are therefore more difficult to catch. Thus, if males with elongated tails cannot catch optimum-sized insects, it may be concluded that elongated tails are handicaps entailing aerodynamic costs.

Weather conditions, especially temperature and precipitation, dramatically affect the abundance of flying insects (Turner 1983). In general, high temperatures and lack of rain are favourable conditions for flight in insects and, consequently, for potential Barn Swallow prey. Calm weather with little or no wind is also favourable for flying insects. Hence, time of day and time of season also affect the abundance of different kinds of prey available to Barn Swallows (Turner 1980). Previous studies have found that the abundance of flying insects is positively correlated with Barn Swallow foraging rates, probably an expected result, but, more interestingly, the relationship between prey abundance and foraging rates improved when only large insects were considered (Turner 1982).

Because weather conditions change with time of season, affecting abundance of prey, differences in feeding rates between first and second broods within the same breeding season might be expected. However, food availability is not the only factor that can explain these differences. Parental care is one of the major time- and energy-consuming activities during the annual cycle (Clutton-Brock 1990), and the physical condition of parents is expected to have deteriorated after first broods as a cost of reproduction (reviewed in Lindén & Møller 1989). Consequently, parents have to face second broods in poorer condition, which would probably affect feeding rates strongly, as provisioning young is generally considered to be the most energy-demanding activity of parental care (Winkler & Wilkinson 1988, Clutton-Brock 1990). As a result, higher feeding rates could be expected for the first brood than the second.

The main aims of this study were (1) to investigate the effect of tail length manipulation in male Barn Swallows on the feeding rates of young (the studies by Møller (1989) and by de Lope and Møller (1993) found different results: the first found no effect whereas the second found decreased feeding rates for males with elongated tails) and (2) to check if this effect differed between first and second broods (to our knowledge this has never been tested before). Moreover, we investigated (3) the possible effect that time of day and time of season had on feeding rates, (4) determining whether this temporal effect might be mediated by the abundance of insects.

METHODS

Study area and species

The study was carried out from February to August 1997 in Seville, southwestern Spain (37°9–13′N, 6°12–20′W). Barn Swallows bred in farmhouses on estates that are usually devoted to extensive cattle raising, and where there are always stables. The area consists of pastures (open or with scattered stands of Holm Oak *Quercus ilex*), crops (cotton, sunflowers) and patches of marshland. There are scattered groups of eucalyptus trees near the farms.

The Barn Swallow is a small, insectivorous passerine (*c.* 20 g) that feeds on the wing. Sexual dimorphism is slight except for the outermost tail feathers, which are typically longer in males than in females. Populations breeding in Europe spend the winter in Africa south of the Sahara. Social monogamy is the rule, with the two sexes building the nest and feeding the young, although only females incubate. Nests are made of mud and are located in buildings or other human constructions, usually in colonies, although solitary nests are not rare. Up to three clutches per breeding season is common in southern Europe, with 4–6 eggs per clutch (for information on the general biology and sexual selection in this species see Cramp 1988, Møller 1994).

Experimental tail length manipulation

Barn Swallows were caught on a weekly basis, beginning on 12 February, just after the first birds were seen in the breeding area, and ending on 6 May. Because birds were all caught every week, no more than 7 days elapsed between arrival and first capture. Thus, date of first capture was considered a good estimator of arrival date. Birds were caught using mist-nets placed at dawn across windows and doors in the rooms (usually stables) where they spent the night (and eventually bred). At the first capture, every individual was weighed (with a Pesola spring balance to the nearest 0.25 g), measured and ringed with a numbered metal band and a unique combination of plastic colour bands, which made individual identification possible from a distance when observing birds in their nests. Males and females in every nest were identified beyond doubt. The length of the right and left outermost tail feathers, central tail feathers, and right and left flattened wings was measured with a ruler to the nearest 0.5 mm. The length of the keel and right and left tarsi was measured with a digital calliper to the nearest 0.01 mm. Tail, wing and tarsus lengths were taken as the means of the left and right characters. All birds were measured by J.J.C. to eliminate interobserver error. At first capture, birds were sexed, mainly according to tail length, although in all cases the sex of the birds was checked by observation of behaviour during incubation.

Male Barn Swallows, when captured for the first time, were randomly assigned to one of three experimental treatments: shortened, elongated or unmanipulated outermost tail feathers. Outermost rectrices were shortened by cutting a 20-mm-long piece 10 mm from the base of the feather and gluing back the apical part to the original base using cyanoacrylate superglue. For elongation, the feathers were cut 10 mm from the base, and the 20-mm-long piece of feather from the shortened group was glued between the apical and the basal pieces. In both treatments, junctions were strengthened by inserting a small piece (2 mm long) of fine entomological pin into the pulp cavity of the rachis. No second control group with feathers cut and glued back without change of length was included in the experiment, because previous studies had shown that the treatment in itself had no effect (Møller 1988a, 1992). Manipulation of the basal part of the feather was performed to allow comparison with previous studies (Møller 1989, de Lope & Møller 1993), despite criticism of this manipulation method (Evans & Thomas 1997, Thomas & Rowe 1997). We did not check whether males were paired or not at the moment when tails were manipulated. In a Danish population of Barn Swallows, the duration of the premating period (from arrival at the breeding grounds to pairing) ranged from 1 to 31 days, 4.8 days on average (Møller 1994, p. 93). Assuming that the premating period is not very different in our Spanish population, it is probable that some males were already paired, and some were not, when tail manipulation took place.

Handling of every bird (measuring, ringing and tail manipulation) lasted about 15 min. After handling, all birds were immediately set free in the same place where they had been caught. Ringing or tail length manipulation had no apparent detrimental effect on birds, as they flew normally when released and resumed regular activities after a few minutes.

Feeding rates

All nests were surveyed every second day to determine clutch and brood size, laying date and hatching date. All observations of chick feeding behaviour were made from a blind (3–8 m from the nest) using binoculars. Male and female identities had been determined for every nest prior to feeding rate observations. Individual identification of the parent feeding the chicks in every feeding bout was usually determined easily by colour rings. However, in some feeding bouts colour rings could not be seen and the sex of the parent was recognized by differences in tail length. These observations took place when chicks were about 12 days old (range 11–13), when nestling growth peaks and feeding rates reach a maximum. Chicks were ringed with numbered metal bands immediately after observations. Chick feeding was not recorded on rainy days. In first broods, the numbers of feeding bouts by males and females were recorded in three 1-h periods on the same day, corresponding to morning (07:00–10:30 h), noon (11:00–14:00 h), and afternoon (15:00–18:30 h) (GMT). There was no chick mortality (partial or total) during the observation day, so the number of chicks for each Barn Swallow pair was always the same for the three periods. In second broods, the number of feeding bouts by males and females was recorded only during a single 1-h period, between 08:00 and 18:00 h GMT.

All Barn Swallows breeding in the same farm foraged in an area nearby, and feeding areas were not defended by individuals (Møller 1988b, and pers. obs.). Thus, differences in feeding rates are not due to differential access to feeding grounds.

Thirty-one male Barn Swallows were included in the study: ten had shortened tails, 11 elongated tails and ten were unmanipulated. Only 29 males were observed for feeding rates in first broods (ten shortened, nine elongated, ten unmanipulated). These observations began on 24 March and ended on 20 June. Some of these males did not have second broods, but two males with elongated tails that had not been observed with first broods were included in second brood observations. These two males nested in stables where researchers had no access during the first broods, but which later became accessible during second broods. As a result, 22 males were observed for feeding rates in second broods (seven shortened, eight elongated, seven unmanipulated). These observations began on 9 May and finished on 18 July. Twenty males were observed in both first and second broods (seven shortened, six elongated, seven unmanipulated).

Insect sampling

The abundance of flying insects was estimated by driving a car down a road crossing the study area and counting insects impacted on the windscreen. Insects were sampled on ten different days, with 10- or 11-day intervals between consecutive samplings, beginning on 5 April and ending on 8 July. Every sampling day included three sampling events, morning, noon and afternoon (see Feeding rates). Both distance (10 km) and speed (90 km/h) were kept constant in every sampling event. Rainy days were avoided. The windscreen was cleaned carefully before every sampling event. Barn Swallows usually feed close to the ground, frequently at only 0.5–2 m (Waugh 1978). Previous studies on food availability for Barn Swallows have also sampled insects at this low height (Bryant & Turner 1982). Insect remains left on the windscreen were not entire, but only body fluids, and were classified as small (< 5 mm) or large (≥ 5 mm). This classification, although arbitrary, was based on previous observations in which most impacts on the windscreen had either a diameter of (1) approximately 1–2 mm, which were relatively abundant and were probably mostly flying aphids (Hemiptera), or (2) > 5 mm, relatively scarce, and probably flying Diptera, Hymenoptera, Lepidoptera, etc. We assume a positive relationship between insect size and the size of the impact left on the windscreen. We do not claim that large and small insects as defined above correspond to large and small insects *sensu* Turner (1982).

Statistical analyses

Statistical analyses were performed according to Sokal and Rohlf (1981) and Siegel and Castellan (1988). Non-parametric statistical tests were applied to discrete ordinal variables (number of broods, eggs or nestlings) and to variables impossible to normalize (male tail length after experimental treatment and number of insects/km). All non-parametric tests were corrected for ties. Otherwise, parametric tests were used throughout. The lengths of external tail feathers and time of day were $\log_{10}$-transformed, while the lengths of the central tail feathers and dates were $x^{0.3}$-transformed to fit the normal distribution. All other variables followed a normal distribution without transformation. Partial correlation values were calculated according to Sokal and Rohlf (1981, p. 656). All statistical tests were two-tailed and the level for significance was set at 0.05.

RESULTS

Experimental tail length manipulation resulted in three groups of males with very different tail lengths

(Kruskal–Wallis test: $H_2 = 25.47$, $n = 31$ males, $P < 0.001$; mean ± se: shortened 78.9 ± 0.8 mm, unmanipulated 104.2 ± 2.7 mm, elongated 121.9 ± 1.6 mm), although the original tail length did not differ significantly among groups (ANOVA: $F_{2,28} = 1.94$, $P = 0.16$). Males in the three experimental groups did not differ significantly in date of first capture (an indicator of arrival date) or in any morphological variable ($F_{2,28} \leq 1.35$, $P \geq 0.27$ in the six cases). Females mated to these males did not differ significantly in date of first laying or in morphological variables ($F_{2,28} \leq 1.53$, $P \geq 0.23$ in the seven cases).

The original tail lengths of males were positively correlated with both the total number of fledglings produced in the breeding season (Spearman correlation: $r_s = 0.450$, $n = 31$, $P = 0.014$) and the number of successful breeding attempts, i.e. number of broods ($r_s = 0.416$, $n = 31$, $P = 0.023$). However, partial correlation between the original tail length and the total number of fledglings, while controlling for the number of successful breeding attempts, was not significant ($r_s = 0.189$, $n = 31$, $P = 0.33$). This suggests that 'originally long-tailed' males produced more offspring during the breeding season simply because they produced more broods, not because their broods were larger.

The number of nestlings did not differ significantly among experimental groups in either first (Kruskal–Wallis test: $H_2 = 0.40$, $n = 29$ nests, $P = 0.82$; mean ± se: shortened 3.9 ± 0.4, unmanipulated 3.9 ± 0.4, elongated 4.2 ± 0.4) or second broods ($H_2 = 0.86$, $n = 22$ nests, $P = 0.65$; mean ± se: shortened 4.4 ± 0.4, unmanipulated 4.3 ± 0.2, elongated 4.5 ± 0.4). First and second broods did not differ significantly in the number of nestlings within breeding pairs (Wilcoxon signed-ranks test: $Z = 0.52$, $n = 20$, $P = 0.61$; mean ± se: first broods 4.3 ± 0.3, second broods 4.5 ± 0.2; only including males with information for both breeding attempts).

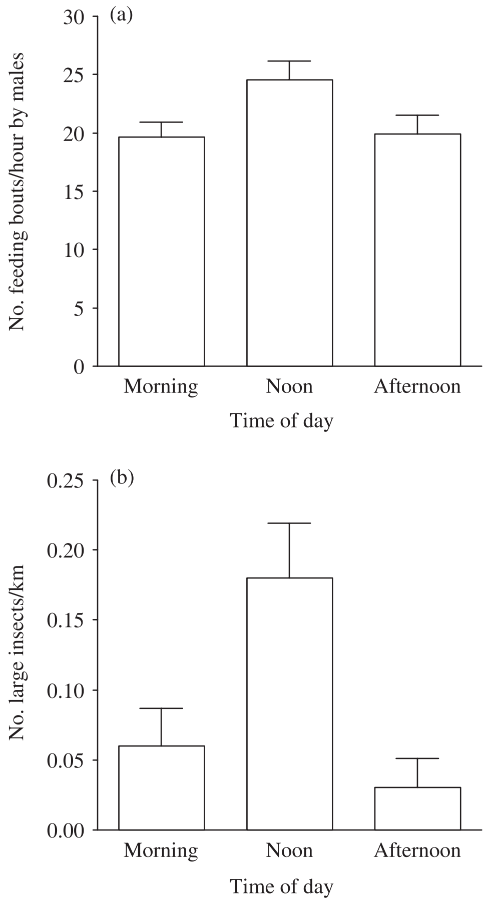

Figure 1. (a) Mean (+se) number of feeding bouts per hour by male Barn Swallows in first broods at different times of day: morning, noon and afternoon (see text for details). Difference between periods was highly significant (repeated-measures ANOVA: $F_{2,56} = 6.24$, $P = 0.004$), with higher feeding rates at noon than in the other two periods (Fisher's LSD *post-hoc* tests: morning vs. noon, $P = 0.003$; morning vs. afternoon, $P = 0.86$; noon vs. afternoon, $P = 0.004$). (b) Mean (+se) number of large insects sampled (per km) at different times of the day. Difference between periods was highly significant (Friedman test: $\chi^2 = 14.87$, $df = 2$, $P < 0.001$), with more large insects sampled around noon than in the other two periods (Wilcoxon signed-ranks tests: morning vs. noon, $Z = 2.64$, $n = 10$, $P = 0.008$; morning vs. afternoon, $Z = -1.13$, $n = 10$, $P = 0.26$; noon vs. afternoon, $Z = -2.72$, $n = 10$, $P = 0.007$; P-values < 0.017 were significant after Bonferroni correction).

Feeding of nestlings

The total number of feeding bouts per hour (by both parents) in first broods depended on the time of day (repeated-measures ANOVA: $F_{2,56} = 7.92$, $P = 0.001$), with higher rates around noon (mean ± se 47.1 ± 3.0), and similarly low rates in the morning (37.4 ± 2.4) and afternoon (39.1 ± 2.8) (Fisher's least-significant difference (LSD) *post-hoc* tests: morning vs. noon, $P < 0.001$; morning vs. afternoon, $P = 0.53$; noon vs. afternoon, $P = 0.003$). Qualitatively similar results were found when feeding bouts per hour by males were considered exclusively (Fig. 1a). Variation at different times of the day in both male and total feeding rates was consistent within pairs (Kendall coefficient of concordance: male feeding rate, $W = 0.64$, $\chi^2 = 53.52$, $df = 28$, $P = 0.005$; total feeding rate, $W = 0.72$, $\chi^2 = 60.76$,

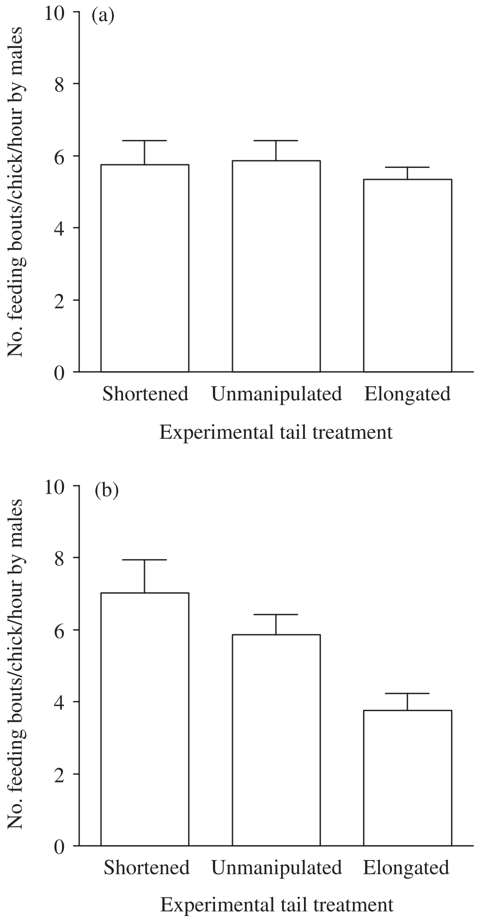

Figure 2. Mean (+se) number of feeding bouts (per chick per hour) by males with different experimental tail treatments: shortened, elongated or unmanipulated (see text for details). (a) First broods: differences among experimental groups were not significant (see statistical test in text). (b) Second broods: differences between experimental groups were significant (ANOVA: $F_{2,19} = 6.42$, $P = 0.007$), males with elongated tails feeding the chicks less often than the other two groups (Fisher's LSD *post-hoc* tests: shortened vs. unmanipulated, $P = 0.24$; shortened vs. elongated, $P = 0.002$; unmanipulated vs. elongated, $P = 0.035$).

$df = 28$, $P < 0.001$). When the three time periods were pooled, no significant differences were found among experimental groups for the following variables: feeding bouts (per chick per hour) by males (Fig. 2a), by females and by both parents, and percentage of feeding bouts by males (ANOVA: $F_{2,26} \leq 0.23$, $P \geq 0.80$ in the four tests). Time of day did not alter this pattern, as shown by separate analyses for every period in which there were no significant differences among experimental groups for any of the previous variables ($F_{2,26} \leq 2.04$, $P \geq 0.15$ in all 12 tests). The original male tail length had no significant influence on male feeding rates in first broods (Pearson correlation: $r = -0.151$, $n = 29$, $P = 0.43$).

In second broods, the number of feeding bouts (per chick per hour) by males differed significantly among experimental groups, males with elongated tails feeding the chicks less often than males in the other two groups (Fig. 2b). Contrary to results in previous studies (de Lope & Møller 1993), females paired to long-tailed males did not compensate for the low feeding rate of their mates; we found no significant difference in the number of feeding bouts (per chick per hour) among the three groups of females (ANOVA: $F_{2,19} = 3.26$, $P = 0.061$; mean ± se, shortened 5.6 ± 0.6, unmanipulated 6.4 ± 0.8, elongated 4.1 ± 0.6; although there was a non-significant trend for females paired to long-tailed males feeding the nestlings less often than females paired to unmanipulated males). As a result, the total number of feeding bouts (per chick per hour) provided by both parents differed significantly in the three experimental groups ($F_{2,19} = 5.53$, $P = 0.013$; mean ± se: shortened 12.6 ± 1.5, unmanipulated 12.2 ± 1.1, elongated 7.8 ± 0.9), with chicks fed by males with experimentally elongated tails receiving food less often than the other two groups of chicks (Fisher's LSD *post-hoc* tests: shortened vs. unmanipulated, $P = 0.80$; shortened vs. elongated, $P = 0.008$; unmanipulated vs. elongated, $P = 0.014$).

Time of day strongly influenced feeding rates by males in both first (Fig. 1a) and second broods (polynomial regression: adjusted $r^2 = 0.450$, $F_{2,19} = 9.58$, $P = 0.001$). In both cases, the feeding rate by males was higher at noon and lower in the morning and afternoon. However, the relationship between the number of feeding bouts (per chick per hour) by males and the experimental treatment (Fig. 2b) still held when controlling for time (ANCOVA: treatment, $F_{2,18} = 6.80$, $P = 0.006$; time, $F_{1,18} = 5.32$, $P = 0.033$). Including treatment, time and time squared in a general linear model analysis showed that all three variables affected feeding rates significantly (Table 1). The variable time squared was included in the analysis because the relationship between the number of feeding bouts by males and the time of day was not linear, but inversely U-shaped (see Fig. 1a).

We found no significant differences between first and second broods in number of feeding bouts (per chick per hour) by males, by females or by both parents (paired *t*-test: $-0.76 \leq t_{19} \leq 0.22$, $P \geq 0.46$ in the three tests; only including pairs with information for

Table 1. General linear model showing the effect of experimental treatment, time of day and time squared on number of feeding bouts (per chick per hour) by male Barn Swallows in second broods.

Source	*df*	Mean square	*F*	*P*
Treatment	2	7.73	3.68	0.047
Time	1	10.54	5.02	0.039
Time^2	1	11.57	5.52	0.031
Error	17	2.10		

both breeding attempts). Original male tail length had no significant influence on male feeding rates in second broods (Pearson correlation: $r = -0.144$, $n = 22$, $P = 0.52$).

Insect estimates

The total number of flying insects sampled (per km) in the study did not depend significantly on the time of day (Friedman test: $\chi^2 = 4.67$, $df = 2$, $P = 0.097$; mean ± se: morning 2.7 ± 0.8, noon 2.9 ± 0.6, afternoon 1.0 ± 0.2) or date (Spearman correlation: $r_s = -0.479$, $n = 10$, $P = 0.15$). However, when restricting analyses exclusively to large insects, a different pattern emerged. Time of day had a significant effect on the number of large insects, which were more abundant around noon than in the morning or the afternoon (Fig. 1b). The number of large insects was also related to date, decreasing in abundance as the season progressed ($r_s = -0.705$, $n = 10$, $P = 0.035$).

DISCUSSION

This study partially corroborates results from a previous study in a different population of Barn Swallows (de Lope & Møller 1993) in which experimental manipulation of male tail length had an effect on the feeding rates of young. To be precise, we found that males with elongated tails fed their nestlings less often than did males with shortened or unmanipulated tails (Fig. 2b). Two mechanisms have traditionally been invoked to explain this result. First, long-tailed males would be more sexually attractive than the other two groups of males, and their females would invest more in parental care, feeding the nestlings more often, so that long-tailed males would not need to feed them so frequently (Burley 1986). However, this explanation does not cover our case, because females paired to long-tailed males did not feed young more often, so reduced male feeding rates were not compensated for and, as a consequence, nestlings in this group were fed less often by their parents than in the other two groups. Secondly, and most probably, tail elongation in male Barn Swallows might have caused flight deficiencies that made insect capture more difficult. This study is not a test of the differential-allocation hypothesis, as we are not sure that all males were paired at the moment of tail-length manipulation, a requisite for such tests (Sheldon 2000). Differences in food abundance might explain why females compensated for reduced male feeding rates in some studies (de Lope & Møller 1993) but not in others (this study), because it might be impossible under conditions of severe food limitation. However, this explanation is merely speculative, as we have no data on food abundance comparable with other studies.

The evolution of long tails in male Barn Swallows has been explained by sexual selection (Møller 1988a), but there is also a non-sexual hypothesis suggesting that long tails may improve flight performance (hereafter natural selection hypothesis; Norberg 1994). Both hypotheses predict that experimental tail elongation will cause flight deficiencies, but predictions based on them concerning experimental tail shortening might differ (depending on the magnitude) (Evans & Thomas 1997). The sexual selection hypothesis posits that the tail has been elongated by sexual selection beyond the aerodynamic optimum, and individuals with shortened tails will improve flight performance if experimental shortening reduces tail length towards that optimum (excessive tail shortening will result in a tail much shorter than the aerodynamic optimum, with consequent flight deficiencies). By contrast, the natural selection hypothesis posits that the flight performance of individuals with shortened tails will suffer because tail length has been displaced from the aerodynamic optimum. In this study, males with shortened or unmanipulated tails showed no significant differences in feeding rates, and it therefore does not support either of the two hypotheses. This result could be explained by recent research suggesting that outermost male Barn Swallow tail feathers are around 10–12 mm longer than the aerodynamic optimum due to sexual selection (Buchanan & Evans 2000, Rowe *et al.* 2001). If this is correct, males with shortened and unmanipulated tails would have tails around 8–10 mm shorter and 10–12 mm longer, respectively, than the aerodynamic optimum. It is possible that similar differences in tail length in both groups of males with regard to the optimal tail length would entail a similar degree of flight deficiency. Finally, we note that aerodynamic costs may have appeared later after we had finished the experiments described here. It is important to bear in mind that results in this study showing no significant effect of experimental tail length manipulation on feeding rates do not necessarily suggest that there is no effect on flight performance. Changes in flight performance may only have caused changes in prey size (e.g. Møller *et al.* 1995), with no change in feeding rates.

Experimental tail elongation in male Barn Swallows reduced feeding rates but, surprisingly, only in second broods. In first broods, we detected no significant effect of tail length manipulation on feeding rates (Fig. 2a). If we had only studied first broods, the result would have been similar to that found by Møller (1989). The difference between first and second broods could have at least three non-exclusive explanations. First, males with experimentally elongated tails may have been able to adjust their parental effort, compensating temporarily, i.e. during first broods, for an imposed handicap by making an extra effort. However, they could not make this extra effort for second broods, or it may simply have been too costly (assuming that any extra effort leads to future cost). A similar pattern, although on a different time scale, has previously been shown for female Barn Swallows. Females with experimentally elongated tails showed no short-term detrimental effect due to tail length manipulation, but their reproduction was less successful in the following year (Cuervo *et al.* 2003). Secondly, the effect of the handicap might be especially important and hence easier to detect under food limitation. Large insects are the preferred prey of Barn Swallows (Turner 1982), and we have shown that the number of large insects in the breeding area decreased as the season progressed. It is possible that large insects became less abundant, reaching levels characteristic of food shortage, late in the breeding season. Total male feeding rates did not differ significantly between first and second broods (see Results), but males with an imposed handicap, i.e. males with experimentally elongated tails, might be especially sensitive to a shortage of preferred prey late in the season. If this explanation is correct, differences in food abundance in different localities might help to explain why males with elongated tails fed their nestlings less often than males with shortened tails in some previous studies (de Lope & Møller 1993) but not in others (Møller 1989). Finally, the effect of the handicap might be especially important when males with elongated tails had already undergone some cost of reproduction. We assume that the physical condition of all males deteriorated after successfully raising first-brood nestlings (Lindén & Møller 1989), but males with an elongated tail would have deteriorated more than the other two groups, having had to face feeding second broods under worse condition.

Variation in feeding rates during the day showed a clear pattern, with feeding bouts more frequent around noon and less frequent in the morning and afternoon (Fig. 1a). This pattern matched variation in abundance of large insects (Fig. 1b), while the total abundance of insects (both small and large) did not differ significantly by time of day. This result suggests that the abundance of large insects might affect feeding rates. In a previous study in a different locality, feeding rates at noon tended to be higher than in the morning or afternoon, but the differences were not statistically significant (Møller 1988b). We speculate that an explanation for the difference between the present and previous study, in which similar feeding rates were observed at different times of the day, might be due to the different diurnal patterns of temperature in northern and southern Europe.

We found no significant differences in feeding rates between first and second broods despite the significant decrease in abundance of large insects as the season progressed. Patterns of feeding rates and abundance of large insects during the breeding season did not match as well as they did when considering variation at different times of the day. Seasonal changes in numbers of large insects were not as pronounced as were changes during the day, and this smaller variation may have resulted in slight differences in feeding rates that our methodology could not detect. Another weakness of this study was that the feeding rate observations and insect sampling very often took place on different days and at different times. That is why we did not relate feeding rates directly to insect abundance, but looked for time patterns in the two variables and to what extent these patterns matched.

In summary, this study shows that experimental elongation of outermost male Barn Swallow tail feathers reduced feeding rates, suggesting that deficiencies in flight were caused by tail length manipulation. However, this reduction in feeding rates was detected only in second broods. Males with elongated tails may have been able to adjust their parental effort, or may have been more sensitive than males in the other experimental groups to late-season food shortages or to deterioration in their physical condition after first broods. Variation in the abundance of large insects at different times of the day matched variation in feeding rates, consistent with the hypothesis that large insects are an important part of the diet of Barn Swallow nestlings.

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