Functional Ecology 2005
19, 828–835

Experimental tail shortening in Barn Swallows (*Hirundo rustica*) affects haematocrit

J. J. CUERVO† and R. M. DE AYALA

Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Calle General Segura 1, E-04001 Almería, Spain

Summary

1. Recent studies in Scotland suggest that the outermost tail feathers of Barn Swallows (*Hirundo rustica* Linnaeus) may be around 10–12 mm longer than the aerodynamic optimum, with sexual selection for long tails accounting for this extra length.
2. To test this hypothesis, we shortened the outermost tail feathers in male and female Barn Swallows in southern Spain by cutting 1, 11 or 21 mm from the tips of the feathers, and checked for change in haematocrit 1 month later. Haematocrit levels were high when birds arrived at the breeding grounds due to an intense effort for flight during migration, but these levels decreased during the breeding season. We predicted that this decrease would be more pronounced when tail length was closer to the aerodynamic optimum (tails shortened by 11 mm), and less pronounced as tail length was displaced from that optimum (tails shortened by 1 or 21 mm).
3. Contrary to expectations, we found that the smaller the experimental reduction in tail length, the more pronounced the decrease in haematocrit. Barn Swallows with little parental effort and originally long tail feathers experienced a more pronounced decrease in haematocrit than individuals with strong parental effort and originally short tail feathers, respectively, although only in the group of birds with tails shortened by 21 mm.
4. These results do not support the hypothesis that outermost tail feathers in Barn Swallows have been elongated because of sexual selection, at least in the population studied, but are consistent with tail length being at an aerodynamic optimum, or very close to it. Differences in tail length among populations might help to understand the disagreement with previous studies.

Key-words: Aerodynamic optimum, flight performance, natural selection, sexual selection, tail streamers

Functional Ecology (2005) **19**, 828–835
doi: 10.1111/j.1365-2435.2005.01018.x

Introduction

Natural and sexual selection often have very different and even opposite effects on trait evolution. However, both processes might have the same effect on a given trait, at least for a certain period of time, making it very difficult to determine which one is responsible for the evolutionary change (e.g. Simmons & Scheepers 1996). One such case is the evolution of the elongated outermost tail feathers in Barn Swallows (*Hirundo rustica* Linnaeus). Elongation of these feathers might have resulted from sexual selection, or natural selection, or both processes simultaneously. As Barn Swallows are aerially insectivorous, this foraging mode would explain the extraordinary importance of morphological traits related to flight in this species.

A long series of studies by Møller *et al*. (1998) have suggested that the outermost tail feathers of male Barn Swallows are secondary sexual characters longer than the aerodynamic optimum. For example, female Barn Swallows preferred to mate with long-tailed males (Møller 1988). Moreover, experimental manipulation of tail length affected survival, males with shortened tails surviving better than males with elongated tails (Møller & de Lope 1994). This finding suggests that carrying long tails is costly for male Barn Swallows. However, other authors (Norberg 1994) have suggested that the distal part of these feathers (the streamer) might have an aerodynamic function as a control device adjusting the leading edge of the feather when the tail is spread and lowered, producing an increase in lift as a result. Nevertheless, this mechanism can work only when the bird is turning with the tail spread, since long streamers in level flight only produce drag (Thomas 1993; Thomas & Balmford 1995). According to Norberg

---

†Author to whom correspondence should be addressed. E-mail: jcuervo@eeza.csic.es

(1994), the aerodynamic advantages of tail streamers would be greater than the disadvantages, so that elongated outermost tail feathers could have evolved exclusively by natural selection.

In most experiments in Barn Swallows by Møller *et al.* in which the tail length was manipulated (e.g. Møller 1988; Saino *et al*. 1997a), the base of the outermost tail feathers was elongated or shortened by 20 mm, while the streamer was allowed to remain intact. This procedure for tail length manipulation has been subject to criticism, because some authors suggest that only the streamer has undergone elongation, the base being similar to other closely related species (Evans & Thomas 1997; Thomas & Rowe 1997). Consequently, to test for a function of long streamers in this species, the streamer should be the portion of the feather manipulated. Later studies (Evans 1998) showed that the aerodynamic consequences of manipulating either the base or the tip were very different, emphasizing the case for streamer manipulation. Moreover, both the natural and sexual selection explanations for long streamers predict that experimental tail elongation entails aerodynamic costs. Thus, experimental tail shortening is the only informative manipulation that can elucidate what mechanism is responsible for streamer evolution: if tail shortening improves aerodynamic performance, tail feathers would be longer than the natural selection optimum, and sexual selection would have played a role in feather evolution (Evans & Thomas 1997; Thomas & Rowe 1997).

The study carried out by Evans (1998) in Scotland also showed that both 20-mm shortening and 20-mm elongation of the outermost tail feathers produced flight deficiencies in Barn Swallows, and concluded that if outermost tail feathers were longer than the aerodynamic optimum, extra length should be less than 20 mm. Hence, subsequent experiments (Buchanan & Evans 2000; Rowe, Evans & Buchanan 2001), also in Scotland, shortened the tip of the streamer in smaller portions, and found aerodynamically superior values for a number of flight components in both males and females when tails were shortened by approximately 10–12 mm. This result suggests that around 10–12 mm in the outermost tail feathers would be due to sexual selection and the rest of the feather length could be attributed to the effects of natural selection. However, these studies are not free from criticism either. For example, in some studies (Evans 1998; Buchanan & Evans 2000) Barn Swallows were filmed ‘entering and leaving the building housing the nest site’ (Buchanan & Evans 2000, p. 230), probably when relevant selective pressures were not acting (for further criticism, see Møller & Barbosa 2001).

The aim of this study was to determine whether the length of the outermost tail feathers in male and female Barn Swallows is only the result of natural selection (aerodynamic optimum), or if sexual selection has contributed to extending streamer length by around 10–12 mm beyond its aerodynamic optimum, as suggested by previous studies in Scotland (see above). We have proceeded with presumably the most appropriate experimental procedure, i.e. shortening the tip of the streamers by different lengths. If the original tail length were optimal according to natural selection, any experimental tail shortening would entail flight deficiencies. On the other hand, if tail length were around 10–12 mm longer than the aerodynamic optimum, experimental tail shortening by approximately 10–12 mm would result in better flight performance than either more or less tail shortening.

There are different ways to check whether tail length manipulation in Barn Swallows has a positive or negative effect on flight performance. Some studies have focused on specific flight parameters (e.g. velocity, acceleration, manoeuvrability), when individuals performed certain manoeuvres (Evans 1998; Buchanan & Evans 2000) or negotiated a flight maze (Rowe *et al*. 2001). Although this approach may help understand the selective forces shaping tail length, it cannot fully account for all the interactions that have taken place in tail length evolution. For example, it is possible that long streamers improve manoeuvrability in turning (Norberg 1994), but, on the other hand, streamers in level flight cause only drag, not lift, thus increasing flight costs (Thomas 1993; Thomas & Balmford 1995). Therefore, we need to know the combined result of all the selective forces related to tail length that affect the Barn Swallow’s flight in the wild. An alternative way to determine if tail length is at an aerodynamic optimum is by assessing a physiological parameter which integrates tail streamer costs and benefits in any individual depending on the relative importance of every kind of flight. One such parameter is haematocrit.

Haematocrit is the proportion of blood volume occupied by packed red blood cells. Haematocrit levels raised by erythropoiesis can be considered an adaptive physiological response to increased oxygen demand (or low oxygen partial pressure) that enhances oxygen uptake efficiency (Gessaman, Johnson & Hoffman 1986). One of the most common causes of increased oxygen demand in birds is intense muscular activity, mainly by muscles involved in flight. Intense effort during flight or energetically costly flight performance produces high haematocrit levels. Barn Swallows arrive at the breeding grounds in Europe after a long migration from their African winter quarters. Such a long journey requires an intense effort for flight, resulting in high haematocrit levels when birds arrive at the breeding grounds, levels that decrease during the breeding season (Saino *et al*. 1997b). We assume that tail length displaced from the aerodynamic optimum impairs flight performance and makes flight more costly, thus resulting in a less pronounced decrease in haematocrit. If experimental shortening of outermost tail feathers by approximately 10–12 mm brings this feather length closer to the aerodynamic optimum, then a more pronounced reduction in haematocrit in individuals with this tail treatment than in other individuals with different tail treatment would be predictable.

There is no evidence that haematocrit is a good estimator of condition in adult Barn Swallows, and therefore we do not know whether haematocrit levels are related to fitness in this species. However, in this study we do not deal with haematocrit levels, but with variations in haematocrit as a result of experimental tail length manipulation. Differences in haematocrit variation among experimental groups would suggest that different tail lengths provoke differences in oxygen demand, implying that birds with some tail length manipulation consume more oxygen and, thus, expend more energy, than with other treatments. We assume that, other things being equal, high energy expenditure due to impaired flight performance will be somehow detrimental, either because of a trade-off between resources allocated to different activities or between present and future allocation of those resources. It would therefore be reasonable for differences in tail length to have some consequences to fitness, providing the basis for selection.

In one study (Saino *et al*. 1997a), the length of the outermost tail feathers in male Barn Swallows was experimentally manipulated by shortening or elongating the base of these feathers by 20 mm, and the change in haematocrit over time was recorded. In that study, haematocrit in males with experimentally elongated tails was maintained during the breeding season, while haematocrit in males with shortened and unmanipulated tails decreased to a similar extent (Saino *et al*. 1997a). The similar decrease in haematocrit for males with shortened and unmanipulated tails does not distinguish whether original tail length was at an aerodynamic optimum or had been elongated beyond that optimum (Evans & Thomas 1997; Thomas & Rowe 1997). There has been no study reducing the length of the distal part of the outermost tail feathers (the streamer) to investigate the consequential change in haematocrit in both male and female Barn Swallows over time.

Materials and methods

FIELD METHODS

The study was carried out during spring–summer 2002 in Almería, in south-eastern Spain (36°45′–37°05′ N, 2°09′–2°31′ W). Barn Swallows breed in farmhouses, solitarily or in small colonies of 2–10 breeding pairs. Birds were caught using mist nets placed at dawn across windows and doors in the rooms where they spent the night. At first capture, every individual was weighed (with a Pesola spring balance to the nearest 0·25 g), measured and provided with a numbered metal ring and a coloured plastic ring. The length of 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. Length of keel and right and left tarsus was measured with a digital calliper to the nearest 0·01 mm. Tail, wing and tarsus length was determined as the mean value of the left and right trait. All birds were measured by the same researcher (J.J.C.) to eliminate any noise in the data due to inter-observer variability. Birds were sexed according to tail length (tail is usually longer in males) and presence of a brood patch (only females incubate).

As many birds as possible were recaptured 30–36 days after first capture (hereafter second capture). In most colonies the first capture took place relatively early in the breeding season (April–May), and the second capture around 1 month later (May–June). But in this second capture, other birds were captured for the first time, and then recaptured (second capture for these birds) around 1 month later (June–July). Thus, some birds were captured for the first time early in the breeding season while other birds were captured for the first time late in the breeding season. Different birds were captured for the first time in different stages of the reproductive cycle. All tail feathers were carefully examined in every capture to detect broken or moulting feathers. All nests were surveyed every second day to identify the parents attending the nest and to determine the number of eggs and nestlings, and dates of laying, hatching and fledging. All nestlings were provided with a numbered metal ring when they were 11–13 days old.

TAIL LENGTH MANIPULATION

Previous studies in Scotland have suggested that the outermost tail feathers in male and female Barn Swallows are around 10 mm (Buchanan & Evans 2000) or 12 mm (Rowe *et al*. 2001) longer than the aerodynamic optimum. We therefore chose to experimentally shorten tail length by 11 mm, in an attempt to make the tail length as close as possible to that supposed optimum. A second experimental treatment consisted in shortening tail length by only 1 mm, thus keeping tail length very close to the original length while still affecting the integrity of the feather, as in the previous treatment. The third experimental treatment consisted in shortening tail length by 21 mm, so that the difference in tail length reduction between birds with tail shortened by 11 mm and the other two experimental groups was the same. We did not include a control group of birds with unmanipulated tails, but we assume that variation in haematocrit in unmanipulated birds would be more like birds with tails shortened by 1 mm than the other two experimental groups.

When captured the first time, all Barn Swallows with tail feathers intact were randomly assigned to one of the three experimental treatments. Manipulation in all treatments consisted in cutting the tip of the outermost tail feathers (at 1, 11 or 21 mm) and trimming the streamer with scissors to imitate its natural rounded end. A number of studies (see Introduction) have pointed out that this kind of tail length manipulation is the most appropriate for understanding the function and evolution of long tails in this species. Very often both birds in a pair were manipulated, either with the same or different experimental treatment. All birds were freed immediately after manipulation in the same place where they had been caught.

HAEMATOCRIT MEASUREMENT

Both after first and second captures, a blood sample was taken from the brachial vein for every bird in a 75-µl capillary tube. Capillaries were then sealed with wax, stored in ice in a cooler and taken to the laboratory, where they were centrifuged at 7700 r.p.m. for 10 min. The haematocrit was measured as the proportion of capillary length occupied by packed red blood cells in relation to capillary length occupied by all blood components. Capillaries were measured with a digital calliper to the nearest 0·01 mm. Following Saino *et al*. (1997a), haematocrit variation between first and second captures (haematocrit in second capture minus haematocrit in first capture) was divided by the number of days elapsed between the two captures (30–36 days) in order to obtain change in haematocrit per day for every individual.

STATISTICAL ANALYSES

A total of 56 Barn Swallows were included in this study: 21 with tail shortened by 1 mm (8 males, 13 females), 19 with tail shortened by 11 mm (10 males, 9 females), and 16 with tail shortened by 21 mm (9 males, 7 females). No birds with broken, missing or moulting tail feathers in either the first or second captures were included in the study. All birds for which information about reproductive performance was incomplete or identification was in doubt were also excluded.

Individuals assigned to the three experimental groups did not differ significantly in haematocrit values at first capture, in morphological traits such as weight or the length of original outermost tail feathers, central tail feathers, wings, tarsus or keel, or in reproductive parameters such as laying date of the first egg or total number of nestlings during the breeding season (one-way ANOVAS, *F*-values always associated with *P*-values greater than 0·10). Experimental tail shortening resulted in three groups of birds with significantly different tail length after manipulation ($F_{2,53} = 11{\cdot}60$, $P < 0{\cdot}001$).

To investigate the possible effect of experimental treatment on variation in haematocrit, we chose change in haematocrit per day as the dependent variable and experimental treatment and five other variables (two continuous and three categorical) that might influence haematocrit as independent variables. The continuous variables were original length of the outermost tail feathers and parental effort. The parental effort index was calculated as the number of nestlings multiplied by the proportion of days with nestlings in the period between the two blood samplings. Provisioning of young is generally considered to be the most energy-demanding activity of parental care (Winkler & Wilkinson 1988; Clutton-Brock 1990), and this index was intended to control for variation in work load among individuals. It has previously been shown that the total number of nestling feedings by both male and female Barn Swallows is positively related to the mass of the brood, i.e. to the number of nestlings (Cuervo *et al*. 1996b). The categorical variables were the sex, the experimental treatment of the mate (tail unmanipulated or shortened by 1, 11 or 21 mm) and date of capture (if birds were captured for the first time early or late in the breeding season; see Field Methods for details). With all these variables and the two-way interactions we performed a backward stepwise general linear model, eliminating all variables and interactions that did not explain a significant amount of the variance from the model. However, the sex was not removed from the model even if it did not explain a significant amount of the variance (see Results). It was not possible to control for colony effect because Barn Swallows included in this study bred in 18 different localities, and mean (SE) number of studied birds per locality was only 3·1 (0·6) (range 1–10). However, it is not probable that differences among colonies affected our results, since the number of birds assigned to experimental groups (*G*-test; $G_{\mathrm{adj}} = 5{\cdot}75$, $P = 0{\cdot}67$) and variation of haematocrit (ANOVA; $F_{4,27} = 1{\cdot}48$, $P = 0{\cdot}24$) did not differ significantly among colonies (only colonies with more than four studied birds were included in these analyses).

Length of original outermost tail feathers and weight were $\log_{10}$-transformed, wing length was x^7-transformed and the index of parental effort was squared-root transformed in order to obtain normal distributions, but all other variables followed a normal distribution without transformation. All statistical tests were two-tailed and the significance level was 0·05.

Results

Mean (SE) length of original outermost tail feathers of the Barn Swallows included in this study was 99·68 (1·27) mm for males ($n = 27$) and 84·53 (0·88) mm for females ($n = 29$). As expected, haematocrit levels in first captures were higher than in second ones (paired *t*-test; $t_{55} = 4{\cdot}40$, $P < 0{\cdot}001$). The only variable significantly related to change in haematocrit per day was experimental treatment (Table 1). The interactions between experimental treatment and original tail length and between experimental treatment and parental effort also explained a significant amount of the variance in the model (Table 1). A significant amount of the variance could not be explained by date of capture, sex, parental effort, experimental treatment of the mate or any of the rest of the two-way interactions.

The results show that the more severe the experimental reduction in tail length, the less pronounced the decrease in haematocrit during the breeding season (Fig. 1). Decrease in haematocrit per day in birds with tail shortened by 1 mm was more pronounced than in birds with tail shortened by 21 mm, but decrease in

Table 1. Variables with a significant effect on change in haematocrit per day after backward stepwise general linear model. Date of capture, experimental treatment of the mate and the rest of two-way interactions were removed from the model because they did not explain a significant amount of the variance. The sex was included in the model even if it did not explain a significant amount of the variance

Source of variation	Mean square	df	*F*	*P*
Experimental treatment	0·027	2,46	4·09	0·023
Sex	0·006	1,46	0·86	0·358
Original tail length	0·005	1,46	0·79	0·378
Parental effort	0·018	1,46	2·69	0·108
Exp. treatment × Original tail length	0·028	2,46	4·25	0·020
Exp. treatment × Parental effort	0·021	2,46	3·24	0·048

haematocrit per day in birds with tail shortened by 11 mm did not differ significantly from the other two experimental groups (Fig. 1). Change in haematocrit per day was related to original tail length only in the group of birds with tail shortened by 21 mm, with long-tailed individuals showing a more pronounced decrease in haematocrit (Table 2). This explains the significant two-way interaction between experimental treatment and original tail length (Table 1). Likewise, change in haematocrit per day was related to parental effort in the group of birds with tail shortened by 21 mm (Table 2), individuals with little parental effort showing a more pronounced decrease in haematocrit than those with a stronger parental effort. However, this relationship was not statistically significant in the other two experimental groups, resulting in a significant two-way interaction between experimental treatment and parental effort (Table 1).

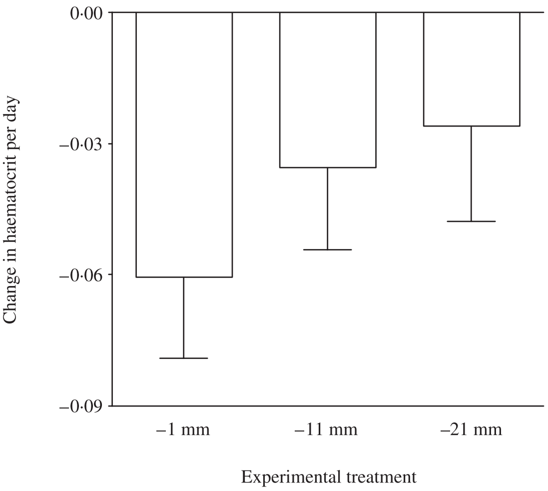

Fig. 1. Change in haematocrit per day in Barn Swallows with outermost tail feathers shortened by 1, 11 and 21 mm, respectively, expressed as adjusted (least squares) means (–SE) from a general linear model including experimental treatment, sex, original tail length, parental effort and the interaction between experimental treatment and original tail length and between experimental treatment and parental effort (see Statistical analyses and Table 1). Decrease in haematocrit per day when tail feathers were shortened by 1 mm was more pronounced than when tail feathers were shortened by 21 mm ($F_{1,30} = 8{\cdot}11$, $P = 0{\cdot}008$). Change in haematocrit per day did not differ significantly between birds with tail shortened by 1 and 11 mm ($F_{1,33} = 1{\cdot}50$, $P = 0{\cdot}23$) or between birds with tail shortened by 11 and 21 mm ($F_{1,28} = 3{\cdot}03$, $P = 0{\cdot}093$).

Discussion

Previous studies in Scotland (Buchanan & Evans 2000; Rowe *et al.* 2001) have suggested that the outermost tail feathers in both male and female Barn Swallows are around 10–12 mm longer than the aerodynamic optimum. Then, approximately 10–12 mm of these feathers would have evolved or been maintained due to sexual selection, and the rest of the feather length would have evolved or been maintained due to natural selection. According to this hypothesis, individuals with a tail shortened by 11 mm would have a tail length closer to the aerodynamic optimum, and we predicted that they would show the most pronounced decrease in haematocrit. Individuals with aerodynamically suboptimal tail length (according to the hypothesis, with tails shortened by 1 and 21 mm) would show suboptimal flight performance and increased flight costs, resulting in a less pronounced decrease in haematocrit. The results of our study do not support this hypothesis. Contrary to expectations, the most pronounced decrease in haematocrit was found in the Barn Swallows with tails shortened by 1 mm, suggesting that this tail length is the closest to the aerodynamic optimum. On the other

Table 2. General linear models showing the effect of sex, original tail length and parental effort on change in haematocrit per day for the three experimental treatments (tail length reduction by 1, 11 or 21 mm). Estimate of effect is shown only for variables explaining a significant amount of the variance

	Tail shortened by 1 mm				Tail shortened by 11 mm				Tail shortened by 21 mm				
Source of variation	Mean square	df	*F*	*P*	Mean square	df	*F*	*P*	Mean square	df	*F*	*P*	Estimate of effect
Sex	0·002	1,17	0·20	0·66	0·006	1,15	0·82	0·38	0·001	1,12	0·11	0·75	–
Original tail length	0·004	1,17	0·55	0·47	0·000	1,15	0·01	0·91	0·027	1,12	5·04	0·044	−1·725
Parental effort	0·007	1,17	0·84	0·37	0·006	1,15	0·81	0·38	0·035	1,12	6·58	0·025	0·010

hand, birds with tails shortened by 21 mm showed the least pronounced decrease in haematocrit, suggesting that tail length had been displaced considerably from the aerodynamic optimum. Individuals with tails shortened by 11 mm showed an intermediate displacement from the aerodynamic optimum compared with the other two experimental groups.

The results of the current study are consistent with the hypothesis that the tail length of Barn Swallows in Almería, in south-eastern Spain, is at an aerodynamic optimum in both sexes. Consequently, this study supports the importance of long streamers in turning, as proposed by Norberg (1994). However, despite the support for natural selection being the selective force shaping tail length, the possibility that sexual selection had a minor role in lengthening tail feathers in this species cannot be ruled out. Individuals with the tail shortened by 1 mm seemed to possess the tail length closest to the aerodynamic optimum (Fig. 1), but we cannot be sure that the aerodynamic optimum was the original tail length. The results of this study are also compatible with sexual selection having lengthened tail streamers a few millimetres (i.e. 1–5 mm) beyond the aerodynamic optimum. Whatever the case may be, sexual selection would only have had very little, if any, influence on tail length, and most (or all) would be explained by natural selection.

Theoretical studies suggest that long streamers in Barn Swallows might be detrimental in level flight, increasing flight costs (Thomas 1993; Thomas & Balmford 1995), but beneficial in tight turnings, improving manoeuvrability (Norberg 1994). Consequently, even if sexual selection has not played a role in the evolution of long streamers in the studied population, experimental tail shortening might have opposite effects on different types of flight. Unfortunately, variation in haematocrit cannot provide information on the effect of experimental tail shortening on every type of flight. Instead, variation in haematocrit could be considered a measure of long-term flight costs as a whole, taking into account the relative importance of every type of flight. We assume there is an aerodynamic optimum for tail length (probably a compromise between different optima for different types of flight), and tail length displaced from the aerodynamic optimum will impair flight performance and will make flight more costly.

One possible clue to understanding the disagreement with previous studies might be the fact that the length of the outermost tail feathers in Barn Swallows differs considerably among populations. In Europe, most morphological traits of Barn Swallows increase with increasing latitude, i.e. Barn Swallows are larger in the north than in the south (Møller 1995). More interestingly, sexual dimorphism in the length of the outermost tail feathers also increases with latitude, while sexual size dimorphism in other morphological traits does not (Møller 1995). Sexual selection would have elongated the outermost tail feathers of male Barn Swallows to a greater degree in the north than in the south of Europe, possibly because of the higher foraging cost of having long tails at low latitudes (Møller 1995). Mean (SE) length of outermost tail feathers in Barn Swallows in Scotland, where these feathers were found to be around 10–12 mm longer than the aerodynamic optimum, is 111·4 (0·8) mm for males ($n = 105$) and 93·6 (0·2) mm for females ($n = 84$) when birds are 2 or more years old, while when birds are 1 year old, it is only 101·5 (1·4) mm for males ($n = 23$) and 90·6 (1·3) mm for females ($n = 16$) (Thompson 1992). In our study in southern Spain, we did not know how old the birds were, but assuming a similar age proportion to the figures shown for the Scottish Barn Swallows, and calculating weighted means for tail length in the Scottish population, we estimate the mean tail length of Barn Swallows in Scotland to be around 10 mm longer for males and 9 mm longer for females than in the population we have studied in southern Spain. Interestingly, the difference in tail length between Barn Swallows in Scotland and southern Spain (9–10 mm) is not very different from the portion of the tail length attributed to sexual selection in the Scottish population (10–12 mm). Therefore, we hypothesize that tail length in Barn Swallows in Almería would be at an aerodynamic optimum or very close to that optimum, while the extra length of Scottish Barn Swallow tail feathers might have evolved due to sexual selection. This explanation could reconcile our study and previous findings.

Other non-exclusive explanations for the different results found in previous studies and this one are also possible. For example, different studies have used very different methods to infer aerodynamic optimum tail length. In previous experiments (Buchanan & Evans 2000; Rowe *et al*. 2001), a number of flight parameters had been estimated when birds performed certain manoeuvres. The optimal tail length for such specific manoeuvres may be around 10–12 mm shorter than actual tail length. However, this optimum may also be very different for different types of manoeuvres (tight turning, level flight, etc.) (Norberg 1994; Thomas & Balmford 1995; Evans & Thomas 1997). The resulting real tail length would be a consequence of the relative importance of all selective forces acting on this trait. Variation in haematocrit could be considered an integral measure of long-term flight costs, and could give us a more accurate approach to forces shaping tail length than any estimate for specific manoeuvres. Long streamers might in fact be important for tight turnings (Norberg 1994), such as those used when pursuing large fast insects, the preferred prey of Barn Swallows (Turner 1982). We can speculate that previous experiments underestimated this importance if turnings performed by birds in these experiments were less tight than those performed when capturing insects (assuming that birds with longer streamers can perform tighter turnings). If this is the case, the 10–12 mm of tail length previously considered aerodynamically suboptimum (Buchanan & Evans 2000; Rowe *et al*. 2001) might have evolved or been maintained to perform very tight turnings, and tail length in Barn Swallows in Scotland would also be at an aerodynamic optimum, or very close to that optimum, as found in our Spanish population. Although this explanation cannot be ruled out, we do not think it is probable, since one of the experiments carried out in Scotland (Rowe *et al*. 2001) forced birds to negotiate a flight maze with the strings at the end of the maze spaced only at 8·5 cm (approximately a quarter of a wingspan of a Barn Swallow), a manoeuvre that requires considerably tight turnings. Moreover, there is so far no evidence that Barn Swallows with longer streamers can perform tighter turnings.

We interpret the difference in haematocrit decrease among the experimental groups as indicative of difference in flight performance, with more severe tail shortening impairing flight to a greater degree than less severe shortening. However, alternative explanations should be examined. It has been shown that the parental effort of female Barn Swallows depends on the attractiveness of their mates: females lay more clutches and feed nestlings more often when they are mated to long-tailed (more attractive) males (de Lope & Møller 1993). Consequently, it might be argued that individuals with the most severe tail length reduction in our study would become less attractive, and their mates less willing to invest in provisioning of young. So these short-tailed (less attractive) individuals would compensate for their mates' reduction in feeding young, and would increase flight effort, resulting in a less pronounced decrease in haematocrit, the result found in the current study (Fig. 1). However, a number of reasons suggest that this explanation is not probable. Firstly, tail length manipulation in male Barn Swallows is not always related to male or female feeding rates (Møller 1989). Secondly, experimental tail length manipulation in female Barn Swallows does not affect their attractiveness or the feeding rates by males or females (Cuervo, de Lope & Møller 1996a; Cuervo *et al*. 1996b). Thirdly, neither the experimental treatment of the mate nor the two-way interaction between the sex and the experimental treatment of the mate showed a significant relationship with the variation in haematocrit (Table 1).

Another important result of this study was that original tail length, i.e. tail length prior to experimental manipulation, was negatively and significantly related to variation in haematocrit in the group of birds with their tails shortened by 21 mm (Table 2). We found that decrease in haematocrit was more pronounced in originally long-tailed individuals than in short-tailed ones. Possible explanations for the negative relationship between original tail length and variation in haematocrit could be that initial haematocrit was higher in long-tailed individuals than in short-tailed ones (Saino *et al*. 1997b) or that long-tailed individuals were in better condition than short-tailed ones, as found in previous studies on male (Møller *et al*. 2003) and even on female (Møller 1994, p. 293) Barn Swallows. However, none of these explanations is probable, because they predict that the relationship between original tail length and variation in haematocrit would also hold in birds with tail shortened by 1 or 11 mm, and this was not the case.

Tail length must have been displaced considerably from the aerodynamic optimum for birds with their tail shortened by 21 mm. Since all birds in the same experimental group had their tails shortened by the same amount (21 mm in this case), the percentage of displacement from the aerodynamic optimum in each individual heavily depended on original tail length. That is to say, within this experimental group, originally long-tailed individuals would have their tails displaced from the aerodynamic optimum relatively less than originally short-tailed individuals. It is reasonable to assume that a high percentage reduction in tail length would affect flight performance to a greater degree than small percentages. Thus, a negative relationship between original tail length and haematocrit variation is to be expected in this experimental group. When tails were shortened by 1 or 11 mm, the difference in percentage of tail reduction between long and short-tailed individuals was much smaller, and a relationship between original tail length and haematocrit variation would be more difficult to find. It might be argued that optimal tail length is not the same for all individuals, for example if there is a positive relationship between the length of the outermost and central tail feathers. However, although this possibility cannot be ruled out, in the sample studied, the length of the outermost tail feathers was not significantly related to the length of central tail feathers (Pearson correlations; males, $n = 27$, $r = -0{\cdot}024$, $P = 0{\cdot}91$; females, $n = 29$, $r = 0{\cdot}245$, $P = 0{\cdot}20$).

In the group of birds with their tail shortened by 21 mm, there was a positive and significant relationship between change in haematocrit per day and the parental effort estimate (Table 2). As expected, decrease in haematocrit was more pronounced in individuals with little parental effort during the breeding season than in individuals with stronger parental effort. However, we would expect this relationship to hold also when tail length had been shortened by 1 or 11 mm, and this was not the case. The relationship between change in haematocrit per day and parental effort was not statistically significant in the two groups of birds with the smallest tail length reduction (Table 2). We can speculate that Barn Swallows would adjust their parental effort according to their own quality and/or condition. If high-quality individuals (or individuals in good condition) could increase their contribution to parental care without increasing their muscular activity, a relationship between intensity of parental effort and variation in haematocrit (mainly determined by variation in muscular effort) would not be expected. However, this adjustment of parental effort to individual quality or condition might be cancelled out if a severe handicap were imposed. According to this reasoning, if variation in haematocrit were related to parental effort only in the group of birds with their tail shortened by 21 mm, it would mean that this experimental treatment imposed the severest handicap, displacing tail length from the aerodynamic optimum to a greater degree than the other two treatments with less severe tail length reduction.

To summarize, this study suggests that tail length of Barn Swallows in Almería (south-eastern Spain) is at an aerodynamic optimum, or very close to it. We hypothesize that different selective pressures in different populations of Barn Swallows might explain differences in tail length among populations and the variety of conclusions reached in different studies with regard to the aerodynamic optimum for tail length in this species.

Acknowledgements

We thank Anders Møller and an anonymous referee for constructive criticism on a previous version of the manuscript, Angela Turner for providing information on tail length in Barn Swallows in Scotland, and the owners of the farmhouses where the study was carried out for allowing access to their properties. Birds were captured and ringed and blood samples taken under licences from Consejería de Medio Ambiente (Junta de Andalucía) and Dirección General de Conservación de la Naturaleza (Ministerio de Medio Ambiente). The study was supported by Junta de Andalucía (Acc. Coord. 2001) and Ministerio de Ciencia y Tecnología (project BOS2001–1717).

References

Buchanan, K.L. & Evans, M.R. (2000) The effect of tail streamer length on aerodynamic performance in the barn swallow. *Behavioral Ecology* **11**, 228–238.

Clutton-Brock, T.H. (1990) *The Evolution of Parental Care*. Princeton University Press, Princeton, NJ.

Cuervo, J.J., de Lope, F. & Møller, A.P. (1996a) The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behavioral Ecology* **7**, 132–136.

Cuervo, J.J., de Lope, F., Møller, A.P. & Moreno, J. (1996b) Energetic cost of tail streamers in the barn swallow (*Hirundo rustica*). *Oecologia* **108**, 252–258.

Evans, M.R. (1998) Selection on swallow tail streamers. *Nature* **394**, 233–234.

Evans, M.R. & Thomas, A.L.R. (1997) Testing the functional significance of tail streamers. *Proceedings of the Royal Society of London B* **264**, 211–217.

Gessaman, J.A., Johnson, J.A. & Hoffman, S.W. (1986) Haematocrits and erythrocyte numbers for Cooper's and sharp-shinned hawks. *Condor* **98**, 95–96.

de Lope, F. & Møller, A.P. (1993) Female reproductive effort depends on the degree of ornamentation of their mates. *Evolution* **47**, 1152–1160.

Møller, A.P. (1988) Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* **332**, 640–642.

Møller, A.P. (1989) Viability costs of male tail ornaments in a swallow. *Nature* **339**, 132–135.

Møller, A.P. (1994) *Sexual Selection and the Barn Swallow*. Oxford University Press, Oxford.

Møller, A.P. (1995) Sexual selection in the barn swallow (*Hirundo rustica*). V. Geographic variation in ornament size. *Journal of Evolutionary Biology* **8**, 3–19.

Møller, A.P. & Barbosa, A. (2001) Flight, fitness and sexual selection. *Behavioral Ecology* **12**, 511–512.

Møller, A.P. & de Lope, F. (1994) Differential costs of a secondary sexual character: an experimental test of the handicap principle. *Evolution* **48**, 1676–1683.

Møller, A.P., Barbosa, A., Cuervo, J.J., de Lope, F., Merino, S. & Saino, N. (1998) Sexual selection and tail streamers in the barn swallow. *Proceedings of the Royal Society of London B* **265**, 409–414.

Møller, A.P., Brohede, J., Cuervo, J.J., de Lope, F. & Primmer, C. (2003) Extrapair paternity in relation to sexual ornamentation, arrival date and condition in a migratory bird. *Behavioral Ecology* **14**, 707–712.

Norberg, R.Å. (1994) Swallow tail streamer is a mechanical device for self-deflection of tail leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proceedings of the Royal Society of London B* **257**, 227–233.

Rowe, L.W., Evans, M.R. & Buchanan, K.L. (2001) The function and evolution of the tail streamer in hirundines. *Behavioral Ecology* **12**, 157–163.

Saino, N., Cuervo, J.J., Krivacek, M., de Lope, F. & Møller, A.P. (1997a) Experimental manipulation of tail ornament size affects the hematocrit of male barn swallows (*Hirundo rustica*). *Oecologia* **110**, 186–190.

Saino, N., Cuervo, J.J., Ninni, P., de Lope, F. & Møller, A.P. (1997b) Haematocrit correlates with tail ornament size in three populations of barn swallow (*Hirundo rustica*). *Functional Ecology* **11**, 604–610.

Simmons, R.E. & Scheepers, L. (1996) Winning by the neck: sexual selection in the evolution of giraffe. *American Naturalist* **148**, 771–786.

Thomas, A.L.R. (1993) On the aerodynamics of birds' tails. *Philosophical Transactions of the Royal Society of London B* **340**, 361–380.

Thomas, A.L.R. & Balmford, A. (1995) How natural selection shapes birds' tails. *American Naturalist* **146**, 848–868.

Thomas, A.L.R. & Rowe, L. (1997) Experimental tests on tail elongation and sexual selection in swallows (*Hirundo rustica*) do not affect the tail streamer and cannot test its function. *Behavioral Ecology* **8**, 580–581.

Thompson, M.L.P. (1992) *Reproductive success and survival of Swallows* (Hirundo rustica): *effects of age and breeding condition*. PhD Thesis, University of Stirling, Stirling,UK.

Turner, A.K. (1982) Optimal foraging by the swallow (*Hirundo rustica*, L.): prey size selection. *Animal Behaviour* **30**, 862–872.

Winkler, D.W. & Wilkinson, G.S. (1988) Parental effort in birds and mammals: theory and measurement. *Oxford Surveys in Evolutionary Biology* **5**, 185–214.

Received 5 January 2005; revised 4 May 2005; accepted 5 May 2005