FEATHER DAMAGE OF LONG TAILS IN BARN SWALLOWS *HIRUNDO RUSTICA*

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Extravagant tails of many male birds are morphological structures affected by both natural and sexual selection. Elongated tail feathers may be more vulnerable to damage than feathers of short length. Feather breakage may thus act as a constraint on the evolution of elongated tails, regardless of mode of selection**.** Feather damage can affect flight performance by producing an asymmetric tail shape that may reduce manoeuvrability and agility. Furthermore, feather asymmetry can reduce male mating success. We studied differences in tail damage in relation to tail length in Barn Swallows *Hirundo rustica* from two populations. Damaged tail feathers were most common in individuals with the longest tails in both populations.

Key words: *Hirundo rustica* – asymmetry - feather damage - flight costs

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INTRODUCTION

The quality of tail feathers may differ among individuals due to differences in diet, for example giving rise to the production of fault bars (Grubb 1989, 1991; Møller 1989). Such variation in feather quality may affect the probability of tail breakage and abrasion, which can be indicators of male quality used in mate selection (Fitzpatrick & Price 1997). Tail damage should have very important consequences for flight performance. Of the various tail shapes, forked tails with streamers seem to be especially vulnerable to damage as streamers receive little support from neighbouring feathers, particularly when the tail is widely spread (Thomas & Balmford 1995). Damage to a single streamer may produce extremely high asymmetry in tail shape, which affects flight performance and therefore flight costs (Møller & Swaddle 1997). If both streamers are damaged, it is unlikely that they break at the same site, thereby causing asymmetry. Tail asymmetry increases the power required for flight at slow speeds and reduces turning performance by affecting the distribution of lift across the aerodynamic surface (Thomas 1993a; Norberg 1994; Møller & Swaddle 1997), and this introduces large rolling and yawing forces and decreases the generated lift. In Barn Swallows *Hirundo rustica*, such decreased manoeuvrability due to tail asymmetry has been demonstrated experimentally (Møller 1991a) and some fitness costs, although smaller than expected, due to asymmetry have been found (Cadee 2000).

Exaggerated tails of birds are functional structures shaped by both natural and sexual selection.

In last years Barn Swallow streamers have attracted the attention of the researchers (Evans & Thomas 1997; Møller *et al*. 1998; Evans 1998; Hedenström & Møller 1999; Evans 1999; Barbosa 1999; Barbosa & 1999a; Barbosa & Møller 1999b; Buchanan & Evans 2000; Matyjasiak *et al*. 2000; Rowe *et al*. 2001; Møller & Barbosa 2001) and therefore information about the costs of this trait is of great interest. Barn Swallows are small (ca 20 g), monogamous, semi-colonial passerines feeding on insects caught on the wing. Sexual size dimorphism is slight with the exception of the outermost feathers of the forked tail. Male tail length is only weakly correlated with structural body size, and individual males are highly consistent in tail length among years (Møller 1991b). Male Barn Swallows attempt to attract a mate by performing displays of their tail ornaments in flight or while perched (Møller 1988). Female Barn Swallows visit several males before making their choice, and males with long and symmetrical tails are preferred over those with short and asymmetrical tails as determined from observations and experiments (Møller 1988, 1990, 1992, 1994a). Long-tailed males also experience a number of other sexual selection advantages (Møller 1990, 1992, 1994a). Nestlings are fed by both adult males and females during three weeks before fledging.

In this paper we relate feather damage in Barn Swallows to tail length and we infer the costs produced by streamer breakage, considering the findings of Norberg (1994) that any tail asymmetry should increase flight costs more than variation in tail shape (Norberg 1994).

METHODS

The studies took place at Kraghede, Denmark (57°N, 10°E), which is an open farmland site with scattered plantations, ponds and hedgerows. The Barn Swallows usually breed on farms either solitarily or in colonies of up to 50 pairs. A detailed description of the population is given in Møller (1994a). The Badajoz study site in Spain (39°N, 7°W) consists of open farmland with scattered groups of trees around farms and rivers. The main crops are grass, maize, and wheat. Barn Swallows breed solitarily or colonially (up to 50 pairs) in farm buildings.

Adult Barn Swallows were captured in mist nets at the breeding sites at both the beginning and the end of the breeding season. On first capture, all birds were provided with a numbered aluminium ring to allow identification. Individuals were sexed from the presence (females) or absence (males) of a brood patch and by the shape of the cloacal protuberance (Svensson 1984). The length of the outermost tail feathers, hereafter tail length, was measured with a ruler to the nearest mm and the condition of the tail of every individual was recorded on each capture. Since the tip of an undamaged streamer is rounded, it is easy to reliably classify feathers as damaged or undamaged depending on the presence or absence of a rounded tip. Recorded damage was substantial resulting in an apparent asymmetry. Records of feather condition were obtained during 1988-1992 in the Kraghede population and during 1994, 1995 and 1997 in Badajoz.. In all cases feather damage caused a high degree of tail asymmetry as almost always only one feather was damaged. Individuals captured several times in different years were used only once in the analyses. Only birds without any damage at first capture were included in the analyses. Since only a very small fraction of birds have damaged tail feathers at the start of the breeding season (Møller 1994a), this exclusion is unlikely to have caused any bias in the remaining sample of birds.

We used logistic regression with damage as the dependent variable, and tail length, sex and country as independent variables. Sex and country were factors in the analyses. The two- and three-way interactions of these variables were first introduced in the model and then deleted backwards if not approaching significance ($P > 0.10$).

Table 1. Results from the logistic regression analysis of damage to the outermost tail feathers of Barn Swallows in relation to tail feather length, country (Denmark or Spain) and sex. The table provides estimates of slopes (b (SE)) and statistical significance for the three main effects and the two- and three-way interactions.

Factor	b	SE	Wald	*P*
Tail	0.041	0.017	5.65	0.017
Country	1.45	1.60	0.81	0.36
Sex	-1.24	1.51	0.66	0.41
Tail * country	-0.002	0.017	0.02	0.87
Tail * sex	0.012	0.016	0.60	0.43
Tail * country * sex	0.003	0.001	2.84	0.09
Intercept	-5.54	1.45	14.57	0.0001

RESULTS AND DISCUSSION

We recorded data for 705 individuals from the Kraghede population and 139 from the Badajoz population. Logistic regression analysis including two- and three-way interactions showed that feather damage was positively related to initial tail length (Table 1). Long-tailed Barn Swallows in both study populations suffered damage to their tail feathers more frequently during the breeding season than short-tailed ones (Fig 1). Smith & Montgomerie (1991) found a similar result although based on a smaller sample size of 48 individuals. They studied the North American population of *Hirundo rustica* that has shorter streamers than the European subspecies, and unlike European males those in North America participate in incubation (Smith & Montgomerie 1992). The same result obtained in both European and North American populations suggests that tail damage is independent of male incubation duties. Tail breakage has been described as a good predictor of reproductive success in monomorphic species with long tails such as the Black-billed Magpie (*Pica pica*) (Fitzpatrick & Price 1997). In Barn Swallows this fact remains to be tested as in the present study feather damage was recorded at the end of the breeding season. However, tail feather damage at the start of the breeding season is more common in short-tailed than in long-tailed males (Møller 1994a). This implies that long-tailed males more frequently have undamaged feathers as compared to short-tailed males, when competing for mating success, but not late during the breeding season.

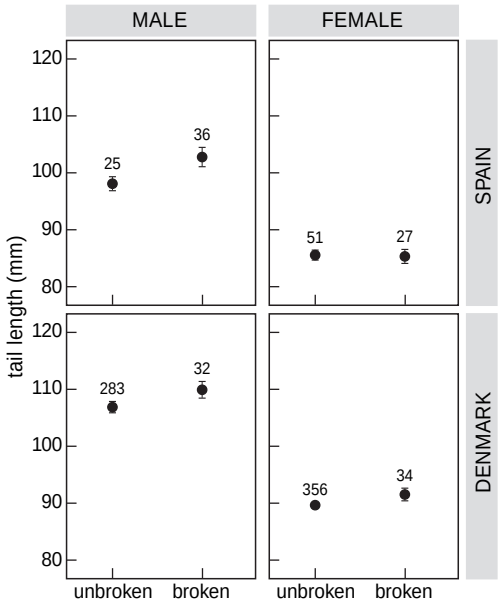

Fig. 1. Differences in original tail length between birds with unbroken and broken tails. Numbers are sample size.

Feather damage has severe aerodynamic consequences similar to those of fluctuating asymmetry in tail length. Forked tails seem to be the optimal shape to maximise lift (Thomas 1993b), but this morphology is highly susceptible to damage

(Thomas & Balmford 1995; Kose & Møller 1999). For example, among a sample of Barn Swallows captured in the South African winter quarters in January 1996 only 10% of adult males (n = 50) and 15% of adult females (n = 46) had undamaged outermost tail feathers (N. Cadée, A. Fridolfsson, H. Ellegren, A.P. Møller and N. Saino unpubl. data). Asymmetry in traits associated with flight morphology is costly in terms of flight performance, particularly during slow speed flight and manoeuvring flight (Thomas 1993a; Norberg 1994). Such aerodynamic effects of asymmetry have been demonstrated experimentally (review in Møller & Swaddle 1997). Cadée (2000) found direct costs on fitness in terms of brood size and nestling quality, although smaller than expected due to wing and tail asymmetry. Our results suggest that such costs might occur more often in long-tailed than in short-tailed males or females, as reflected by the results of the logistic regression analysis. It is possible that an interaction exists between costs of long tails and feather quality due to drag caused by long tails and increased yaw and rolling forces due to asymmetry produced by damage. Thomas (1993a) predicted that asymmetry in tail length should be more costly for males with the longest traits. Therefore, asymmetry costs of tail length should be lower for individuals with shorter tails such as females or short-tailed males. Swaddle & Witter (1994) proposed a possible trade-off between size and symmetry of tail ornaments that could also be applied to the case of artificial asymmetry produced by damage. This possibility is supported by the findings of Evans *et al.* (1994) for Streamertail *Trochilus polytmus*, in which asymmetry was unimportant for manoeuvrability when streamers were short, but as streamer length increased, similar levels of asymmetry significantly reduced manoeuvrability (Evans *et al*. 1994).

Asymmetry costs of long tails could be more important than the possible benefits of increased lift by long tails, as feather asymmetry creates asymmetry of induced drag that would have to be compensated by changes in wing attitude, thereby potentially increasing total drag (Norberg 1994). Norberg (1994) stated that there is a much stronger effect of asymmetry than previously recognised, as tail streamers modify tail profile shape during manoeuvres. This precludes benefits through the Norberg effect when breakage has occurred. If we accept the hypothesised benefits of long tails through the Norberg effect, the cost of asymmetry as a consequence of such aerodynamic effects must also be accepted as stated by Norberg (Norberg 1994). Asymmetry produced by feather breakage is on average much greater than natural tail asymmetry. Therefore, feather breakage could be a constraint limiting tail length.

Møller (1994a) reported that short-tailed male Barn Swallows had more fault bars than long-tailed males, and that the frequency of damaged tail feathers decreased with increasing tail length at the start of the breeding season, indicating different phenotypic quality of feathers of short- and long-tailed males. Thus, feather quality through the frequency of fault bars directly influence feather breakage at the start of the breeding season. Later feather damage during the breeding season cannot be attributed to differences in feather quality, and we hence must invoke differences in behaviour of short- and long-tailed males. We hypothesise that feather damage incurred during fighting for competition for mates or during paternity guards (Møller 1994a) are responsible for the differential increase in feather damage among long-tailed male Barn Swallows. The discrepancy between the results presented here and those on feather damage reported by Møller (1994a) arises because the latter only reported feather damage at first capture, but not at the end of the breeding season. Long-tailed males are thus more likely than short-tailed ones to experience a mating advantage of long tails at the start of the breeding season, while paying an aerodynamic cost at the end of the season.

In conclusion, the positive relationship between the probability of tail feather damage in long-tailed male Barn Swallows during the breeding season suggests an increase in aerodynamic costs for long-tailed males. Such costs could represent a constraint on the evolution of tail length.

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SAMENVATTING

Bij veel vogelsoorten hebben de mannetjes extravagant lange staarten, die waarschijnlijk het product zijn van zowel natuurlijke als seksuele selectie. Natuurlijke selectie zal een staart zo 'bouwen' dat het de overlevingswaarde van zijn drager verhoogt. Seksuele selectie daarentegen leidt juist tot staarten die in principe nadelig zijn voor de drager. Mannetjes die zich zo'n staart kunnen veroorloven, moeten dus van goede kwaliteit zijn, waardoor ze voor vrouwtjes aantrekkelijk zijn. Deze korte studie draagt nieuwe munitie aan in het

langlopende debat tussen voorstanders van beide typen van selectie. Mannetjes van de Boerenzwaluw *Hirundo rustica* hebben verlengde buitenste staartpennen. Eerdere studies hebben duidelijk laten zien dat dit een kenmerk is waar vrouwtjes hun partner op kiezen. Het nadeel van deze staartpennen is echter dat ze ook gemakkelijk kunnen breken, wat mogelijk, naast een aërodynamisch nadeel bij het vliegen, een reductie in manoeuvreerbaarheid oplevert. In een Deens en een Spaans studiegebied was de kans op gebroken staartpennen het grootst bij mannetjes met langere staarten. Dit wijst erop dat het hebben van een extra lange staart inderdaad een handicap kan zijn. (CB)

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