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ORIGINAL ARTICLE

**Oddmund Kleven · Frode Jacobsen ·
Rasa Izadnegahdar · Raleigh J. Robertson ·
Jan T. Lifjeld**

Male tail streamer length predicts fertilization success in the North American barn swallow (*Hirundo rustica erythrogaster*)

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Abstract In socially monogamous species, extra-pair paternity has the potential to increase the variance in male reproductive success, thereby affecting the opportunity for sexual selection on male extravagant ornamentation. In the European barn swallow (*Hirundo rustica rustica*), the tail streamer length is a sexually selected male ornament and an honest indicator of viability. The North American barn swallow (*Hirundo rustica erythrogaster*) also shows sexual dimorphism in tail streamer length, but whether this trait holds the same signalling function in this subspecies is a controversial issue, and the available literature is presently scarce. Here, we present data on paternity in the North American barn swallow, including a complete sampling of extra-pair sires in four colonies. We analysed how extra-pair paternity affected the variance in male fertilization success and examined whether male tail streamer (i.e. the outermost tail feather) length correlated with fertilization success (n=86 males). Extra-pair paternity constituted 31% of all offspring and significantly increased the variance in male fertilization success. The number of offspring sired by extra-pair males accounted for almost half of the total variance in male fertilization success. Males with naturally long tail streamers had a higher fertilization success than males with shorter tail streamers, and this pattern was mainly caused by a higher extra-pair success for males with long tail streamers. Males with long tail streamers also paired with early breeding females in prime body condition. These results are consistent with the idea that there is directional sexual selection on male tail streamer length, possibly mediated through male extra-pair mating success or the timing of breeding onset.

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O. Kleven (✉) · F. Jacobsen · J. T. Lifjeld
Natural History Museum, University of Oslo,
P.O. Box 1172, Blindern,
0318 Oslo, Norway
e-mail: oddmund.kleven@nhm.uio.no

R. Izadnegahdar · R. J. Robertson
Department of Biology, Queen's University,
Kingston, Ontario, K7L 3N6, Canada

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Introduction

Sexual selection can arise whenever there is non-random variance in individual reproductive success among members of one sex (Arnold and Wade 1984; Andersson 1994), and the trait in question is associated with intrasexual competition or intersexual choice (Darwin 1871). As males usually compete for access to females, and not vice versa, sexual selection is usually more intense on males than on females, and this gives rise to sexual dimorphism (Darwin 1871; Andersson 1994). Extravagant ornamentation and sexual dimorphism are more easily explained in polygynous mating systems with high variance in male mating success, but the presence of such traits in many monogamous species suggests that sexual selection can also operate here (Darwin 1871). Several possible mechanisms for sexual selection in socially monogamous species have been proposed (reviewed in Kirkpatrick et al. 1990; Birkhead and Møller 1992), and two of the main mechanisms are sexual selection through timing of breeding (O'Donald 1972; Kirkpatrick et al. 1990) and sexual selection through extra-pair mating (Møller 1988; Webster et al. 1995).

According to the timing of breeding hypothesis, females arriving at the breeding grounds early in the season choose the most ornamented males. These early breeding females are able to produce more or higher-quality offspring during a breeding season (Verhulst and Tinbergen 1991; Brinkhof et al. 1993), hence their well-ornamented partners will experience a reproductive advantage compared to less-ornamented males. The hypothesis is founded on a broad theoretical background (e.g. O'Donald 1972; Price et al. 1988; Kirkpatrick et al. 1990) and has received some empirical support (e.g. Møller 1988; McGraw et al. 2001; Thusius et al. 2001).

Extra-pair mating is also an important selective component in the evolution of male extravagant ornamentation. Genetic parentage analyses have revealed that extra-pair mating is widespread among socially monogamous species, especially so in birds (reviewed in Griffith et al. 2002). Extra-pair fertilizations may give reproductive benefits to males by increasing their number of offspring sired. From a female perspective, multiple mating can be seen as a means to enhance the probability or quality of fertilizations, and thereby circumvent the constraints imposed by social monogamy (Møller 1994; Petrie and Kempenaers 1998). Extra-pair mating, whether it is a male- or female-driven behaviour, has the potential to increase the variance in male reproductive success (reviewed in Møller and Ninni 1998, but see Freeman-Gallant et al. 2005) as long as extra-pair fertilizations are not balanced by a similar loss of within-pair paternity. Hence, extra-pair mating can influence the opportunity for sexual selection on extravagant male ornaments. Previous studies in socially monogamous species have revealed a relationship between phenotypic traits and extra-pair fertilization success (e.g. Kempenaers et al. 1992; Hasselquist et al. 1996; Saino et al. 1997; Sheldon et al. 1997, but see, e.g. Weatherhead and Boag 1995).

The socially monogamous barn swallow (*Hirundo rustica*) has become a model species in sexual selection due to the many studies in Europe indicating a female preference for long tail streamers in males. A positive correlation has been found between male natural tail streamer length and both within-pair paternity (Møller and Tegelström 1997) and realised (sum of within-pair and extra-pair) success (Saino et al. 1997). Tail manipulation experiments have further revealed that males with elongated tails obtain a pair mate (i.e. breeding partner) earlier, have higher paternity in their own brood and are more successful in obtaining extra-pair fertilizations than males in the control groups or males with shortened tail streamer length (e.g. Møller 1988, 1994; Saino et al. 1997).

Male North American barn swallows (*H. r. erythrogaster*), like their European counterparts (*H. r. rustica*), have longer tail streamers than females (Smith and Montgomerie 1991), but it is not yet known if males with long tail streamers have higher fertilization success, as shown for the European barn swallow (e.g. Saino et al. 1997). The only study of paternity in the North American barn swallow is experimental (Smith et al. 1991). In that study, paternity loss was higher for males with elongated tail streamer length than for males with shortened tail streamer length, but paternity correlated positively with the original tail streamer length (Smith et al. 1991), thus contrasting results from studies on the European barn swallow (e.g. Møller and Tegelström 1997; Saino et al. 1997). The study by Smith et al. (1991) was, however, based on a relatively small sample (n=11 broods) and did not assign paternity to extra-pair offspring, so it is unclear whether male tail streamer length affected realised fertilization success.

We have two main aims in the present study. First, we want to investigate whether extra-pair paternity has an effect on the opportunity for sexual selection by estimating the standardized variance in male fertilization success (Arnold and Wade 1984) and partitioning this variance into within-pair and extra-pair components (Webster et al. 1995). In general, good estimates of such variance components are lacking (see e.g. Freeman-Gallant et al. 2005) due to difficulties in identifying extra-pair sires, and as far as we are aware, these kinds of data have previously not been published for barn swallows. We use microsatellite DNA markers to analyse blood samples from 86 families, enabling us to determine paternity and to identify the sires of all offspring. Second, we want to determine if differences exist between male and female tail streamer length as well as examine the relationships between male tail streamer length and (1) female condition, (2) onset of breeding and (3) fertilization success.

Materials and methods

Study site and study species

The barn swallow is a small (≈19 g), short-lived insectivorous passerine species. It is a migratory bird that breeds, either solitarily or in colonies, in large parts of the Holarctic. Females lay three to seven eggs in a brood, and pairs raise one to two broods per season. Females incubate the eggs (in the North American barn swallow, males also partly assist), while both parents care for the young. Hatching is synchronous, usually within 24 h, and the young leave the nest approximately 20 days post-hatching (Møller 1994; Brown and Brown 1999).

We studied North American barn swallows from late April to mid-July 2003 in the vicinity of the Queen's University Biological Station (44°34′N, 76°19′W) in Ontario, Canada. We monitored four colonies situated far from each other (closest distance 4.7 km) and with no observed interaction between individuals from the different colonies. The colonies ranged in size from 8 to 61 breeding pairs. Adults were captured with mist nets at the breeding sites and banded with one numbered aluminium band. To facilitate individual identification, the adults were banded with one plastic colour band and painted on the right wing (with acrylic paint) at three small spots by using a unique colour combination. Upon capture, we measured the entire length of the right and left tail streamers (to the nearest 0.5 mm, using a ruler with a thin pin zero stop), and in the following statistical analyses, we have used the mean of these two values. A subset of individuals were measured twice, revealing that the separate measures of tail streamer length were highly repeatable (r=0.99, $F_{29,59}$=48.9, P<0.001; Lessells and Boag 1987). In the case of a broken (n=3) or missing (n=2) character, the intact or the remaining one was used. Furthermore, we measured body mass (using a Pesola spring balance, ±0.25 g) and tarsus length (to the nearest 0.01 mm, using a digital calliper). All measurements were performed by one person only (O.K.). We sampled a small amount of blood (ca. 15 μl) by brachial venipuncture, diluted and stored in lysis buffer for later use in genetic analyses. Our capture and handling of the birds did not seem to have any adverse effects on their survival prospects. Recapture data of this long-distance migratory bird species revealed that 53% (122/232; Kleven et al. in press-a) of all captured adult individuals survived and returned to the same colony the year after, which is a slightly higher rate compared to that found in other studies of the North American barn swallow (e.g. Shields 1984; Brown and Brown 1999).

Adults were sexed in the field and later sexed conclusively by molecular methods (see Kleven et al. in press-b). Briefly, males and females were distinguished according to the shape of the cloacal protuberance (Svensson 1984), the presence (females) or absence (males) of a brood patch, a tail length formula (Smith and Montgomerie 1991) and through observations of their breeding behaviour (e.g. display and song). Ultimately, all adults were sexed with the P2/P8 primers from the CHD gene (Griffiths et al. 1998).

The colonies were visited daily (with a few exceptions), and the breeding pairs were identified through observations of nest building, brooding and nestling provisioning. No cases of polygyny were observed. We monitored most of the nests prior to egg laying until the young were 16 days post-hatch. We collected blood (2–25 μl) from the nestlings by puncturing either the brachial or the medial metatarsal vein 3 days after hatching. Unhatched eggs and dead young found in the nests were collected, and tissues from these samples were stored in 70% ethanol. The field work ended in mid-July, after all first broods had been sampled. The study therefore does not include a few re-nesting attempts (n=4), following nesting failures earlier in the season, or regular second broods.

Genetic analyses

Paternity was assigned using nine polymorphic microsatellite markers. Detailed information about the markers, their variability and paternity determination are presented elsewhere (Kleven et al. in press-a,b). Briefly, we extracted DNA with a QIAamp DNA mini kit (Qiagen, Venlo, The Netherlands) and amplified the microsatellites by polymerase chain reaction (PCR). PCR products were run on an ABI 3100 sequencer (Applied Biosystems, Foster City, USA), and the fragment analysis data were analysed with GeneMapper v3.0 (Applied Biosystems). The combined exclusion probability (Jamieson 1994) for the nine markers was higher than 0.9999, and we defined young as being sired by an extra-pair male if two or more of the markers excluded the putative father as genetic father.

Male fertilization success

Fertilization success was based on the number of young genotyped. We obtained genotypes from 392 out of a total of 443 eggs laid in the 86 nests. The deviation in the number of young genotyped compared with the number of eggs laid was due to infertile eggs (4%), eggs that went missing prior to hatching (4%) and young that went missing between hatching and the time of blood sampling (3%). Apparent fertilization success was calculated by the number of all young genotyped in a brood, while realised fertilization success was calculated by the number of within-pair and extra-pair young a male sired. An index of the opportunity for sexual selection, for both apparent (I_{sa}) and realised (I_{sr}) success, was calculated by dividing the variance in male fertilization success by the square of the mean success (Wade and Arnold 1980). We also partitioned the variance according to the method described in Webster et al. (1995) and present the variance components due to within-pair paternity, extra-pair paternity and the covariance between these two components. Six males that were not breeding in any of our colonies, but who obtained extra-pair fertilizations, were excluded in these calculations.

Statistical analyses

Tail streamer length and date of breeding onset (i.e. egg laying) were log-transformed before statistical analyses to obtain approximate normal distributions. The likelihood of losing or gaining paternity (yes/no) was analysed with generalised linear models (GLMs) with a binomial error distribution. Proportion of within-pair young sired was analysed with GLMs using binomial errors and logit link, with number of within-pair young as a response variable and brood size as the binomial denominator. The variables "number of extra-pair young sired" and "realised fertiliza-

Table 1 Paternity and the variance in male fertilization success in four colonies of the North American barn swallow

Colony (no. of broods)	EP broods ratio	EPY ratio	I_{sa}	I_{sr}	I_{sr}/I_{sa}	Total variance ratio		
						WPP	EPP	Covar
Barn (n=9)	0.44	0.21 (8/39)	0.080	0.156	2.0	0.97	0.61	−0.58
Boathouse (n=8)	0.50	0.26 (10/38)	0.073	0.529	7.2	0.32	0.43	0.25
Loughborough Bridge (n=53)	0.53	0.31 (74/235)	0.073	0.446	6.1	0.39	0.58	0.03
Zealand sand dome (n=16)	0.44	0.37 (29/79)	0.041	0.999	24.4	0.23	0.33	0.44
Combined (n=86)	0.50	0.31 (121/391)	0.067	0.533	8.0	0.33	0.48	0.19

The frequency of extrapair paternity is shown as the proportion of broods with extra-pair young (EP broods ratio) and as the proportion of extra-pair young among all broods (EPY ratio). The fertilization success of males is shown by the standardized variance in apparent and realised success. The total variance is divided into three components: within-pair paternity success, extra-pair paternity success and the covariance between these two components

EP Extra-pair, *EPY* extra-pair young, I_{sa}, standardized variance in apparent success, I_{sr} standardized variance in realised success, *WPP* within-pair paternity, *EPP* extra-pair paternity, *Covar* covariance between WPP and EPP

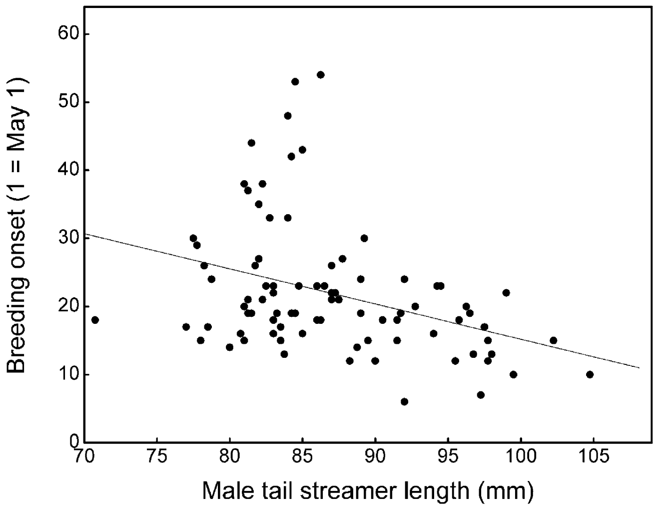

Fig. 1 Breeding onset (i.e. the date when the first egg in a brood was laid) of North American barn swallows (n=86) in relation to male tail streamer length. A regression *line* is indicated

tion success" showed an approximate Poisson and a Poisson distribution, respectively. These response variables were therefore analysed with GLMs with a Poisson error distribution. Non-parametric tests were used when comparing tail length of males and females (due to unequal variances) and when comparing tail length of cuckolder and cuckoldee (due to non-normality of the paired differences). Female body condition was calculated as body mass (g) divided by tarsus length (mm). As we lack some biometrical data for a few females, the sample sizes vary accordingly. All tests were two-tailed, and the significance level was set to 0.05. Statistical analyses were performed with GLMStat v5.5 http://www.glmstat.com) and STATISTICA v6.1 (StatSoft, Inc., Tulsa, USA).

Results

Patterns of paternity

We found that extra-pair paternity occurred frequently, as 50% (43/86) of the broods contained at least one extra-pair young, and a total of 31.0% (121/391) of the offspring were sired by an extra-pair male (Table 1). In 35 out of the 43 broods containing extra-pair young, more than one of the young were sired extra-pair. In 13 of these broods, we identified two extra-pair sires, and in one brood we identified three extra-pair sires. We identified the genetic father of all the young, and the males that gained extra-pair paternity were either breeding in the colony where they sired extra-pair offspring (n=34 males) or not breeding in any of the four colonies (n=6 males). These six latter males, initially caught in the colony where they sired extra-pair offspring, were either breeding nearby or were unpaired males (floaters); three of these males were recaptured in the same colony the year after, with two of these three as paired males (O. Kleven, unpublished data).

Variance in male fertilization success

Males that sired extra-pair offspring had a higher realised fertilization success (mean±SE 6.5±0.6 young, n=34) compared to males with no extra-pair success (3.0±0.3 young, n=52; Mann–Whitney U test Z=4.9, P<0.001). Hence, extra-pair paternity had a significant impact on the variance in male fertilization success (F ratio test F=3.2, P<0.001, n=86), and the opportunity for sexual selection was 8.0 times higher for male realised rather than apparent success (Table 1). Approximately half of the variance in male realised fertilization success was explained by extra-pair paternity, while within-pair paternity explained one third. The covariance between these two components was positive and amounted to 19% (Table 1). There was variation among the colonies in the opportunity for sexual selection and in the relative contribution of the partitioned variance components (Table 1).

Tail streamer length and paternity

Males had longer tail streamers than females (86.9 mm±0.7 SE, n=86 vs 76.3±0.5, n=82; Mann–Whitney U test Z=9.2, P<0.001). There was no assortative mating based on tail streamer length (Pearson correlation r=0.12, P=0.28, n=82), but males with the longest tail streamers were paired with females in prime body condition (r=0.25, P=0.027, n=81), and these males started to breed (first egg date of social mate) earlier in the season (r=−0.42, P<0.001, n=86; Fig. 1).

The tail streamer length in males was not a predictor of the likelihood of being cuckolded or of the proportion of

Table 2 Male tail streamer length in relation to within-pair, extra-pair and realised fertilization success in the North American barn swallow

	Within-pair paternity				Extra-pair paternity				Realised success	
	Likelihood of losing paternity[a]		Proportion of young sired[b]		Likelihood of gaining paternity[a]		Number of young sired[c]		Number of young sired[c]	
	χ^2	P	F	P	χ^2	P	χ^2	P	χ^2	P
Tail streamer length (n=86 males)	0.1	0.81	0.8	0.38	6.4	0.012	28.2	<0.001	10.6	0.001

[a] Generalised linear model with binomial error distribution and logit link

[b] Generalised linear model with binomial error distribution and logit link; brood size is used as a binomial denominator. F ratio statistics is shown

[c] Generalised linear model with Poisson error distribution and logarithm link

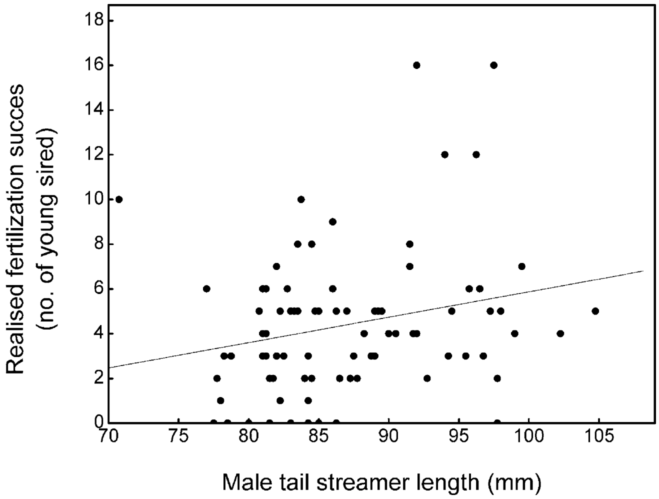

Fig. 2 Realised fertilization success (the sum of within-pair and extra-pair young sired) of North American barn swallow males (n=86) in relation to their tail streamer length. A regression *line* is indicated

young sired in their own brood (Table 2). However, the likelihood of obtaining extra-pair fertilizations and the number of extra-pair young sired increased with the length of the tail streamers in males (Table 2). Males with long tail streamers had a higher realised fertilization success than shorter-tailed males (Table 2 and Fig. 2), and a pairwise comparison showed that extra-pair males had longer tail streamers (90.2±1.0 mm) than the males they cuckolded (87.1±1.1 mm, Wilcoxon matched pair test Z=2.3, P=0.020, n=43).

Discussion

In this study, we were able to identify the sires of all offspring, and thus, we were able to obtain an accurate estimate of the total fertilization success for each male. Extra-pair fertilizations increased the standardized variance in male realised fertilization success eightfold compared to the apparent success. This result is in accordance with several other studies of socially monogamous species documenting that extra-pair paternity increases the opportunity for sexual selection (Webster et al. 1995; Yezerinac et al. 1995; Johnsen et al. 2001; Richardson and Burke 2001; Delhey et al. 2003; Whittingham and Dunn 2005). However, it has recently been suggested that the incomplete sampling of extra-pair sires in most previous studies may have created a bias (i.e. to high values) in estimates of the opportunity for sexual selection resulting from extra-pair mating (Freeman-Gallant et al. 2005). In contrast, our data reveal that even with a complete knowledge of extra-pair sires, extra-pair paternity may still have a significant impact on the opportunity for sexual selection. Extra-pair paternity was the single variance component that contributed most (48%) to the fertilization success of males. Our analyses further revealed that the tail streamer length of males was a significant predictor of the realised fertilization success, mainly as males with naturally long tail streamers had greater extra-pair fertilization success. Our results therefore suggest that extra-pair mating increases the opportunity for sexual selection on male tail streamer length.

The frequency of extra-pair paternity that we found (31% of young) was similar to that found by Smith et al. (1991) (29% of young) and was also similar to those found for the European barn swallow (e.g. 28% in Møller and Tegelström 1997; 33% in Saino et al. 1997; and 18% in Møller et al. 2003). This frequency of extra-pair paternity is relatively high compared to many other socially monogamous bird species (reviewed in Griffith et al. 2002).

We found that half of the total variance in male fertilization success was attributable to extra-pair success, while within-pair paternity explained about only one third. The covariance between these two components was positive (19%), suggesting that males who were successful in securing within-pair paternity had a higher extra-pair success. The variance component from extra-pair paternity is considerably higher than most of the figures reported in two recent reviews of various passerines (Freeman-Gallant et al. 2005; Whittingham and Dunn 2005). This is an indication that extra-pair mating success is more skewed in the North American barn swallow than in many other passerines with frequent extra-pair mating. A possible factor contributing to this skew is colonial breeding, which allows successful males to gain access to many extra-pair mating partners. This is in contrast to a more spaced territorial system, in which extra-pair matings usually occur among neighbours (e.g. Yezerinac et al. 1995; Webster et al. 2001; Mennill et al. 2004; Freeman-Gallant et al. 2005).

A potential bias in our variance estimates may exist due to the inclusion of first broods only (e.g. Poirier et al. 2004), since approximately 30% of the pairs in our study area have second broods (Smith and Montgomerie 1991). As the number of fertile females are fewer, and the clutch sizes are smaller later in the season (O. Kleven, unpublished data), the likelihood for males to obtain extra-pair fertilizations is decreasing throughout the season. Hence, the opportunity for sexual selection due to extra-pair paternity as compared to within-pair paternity may be less than reported here. However, as indicated in a recent study of Savannah sparrows (*Passerculus sandwichensis*), the opportunity for sexual selection does not seem to differ between first and second broods (Freeman-Gallant et al. 2005).

Consistent with previous studies in both Europe and North America (e.g. Smith and Montgomerie 1991; Møller 1994; Safran and McGraw 2004), we found sexual dimorphism in tail streamer length with longer tail ornaments in males than females. The length of tail streamers and the degree of sexual size dimorphism in this plumage trait shows clinal variation and increases with increasing latitude (e.g. Møller 1994; Brown and Brown 1999). In our study population, male tail streamer length was, on average, 13% longer than in females, while in Europe, the figures of sexual tail dimorphism ranges from 6 to 25% (Møller 1994). While we might have expected assortative mating with regard to tail streamer length, this did not occur. Possibly, tail streamer length may not reflect quality in females, as it seems to in males. Moreover, female tail streamer length may not be subject to male mate choice.

A negative association between male tail streamer length and the date of breeding onset (i.e. egg laying by social mate) has previously been reported in a tail manipulation study of the North American barn swallow (Smith and Montgomerie 1991), while a recent correlative study failed to find an association (Safran and McGraw 2004). Differences in these results between our study and that of Safran and McGraw (2004) suggests that there might be local differences in selection pressures on tail streamer length within North America rather than between the North American and European subspecies. Further research needs to be conducted to verify these seemingly opposing, yet potentially highly intriguing, findings. Previous studies of the European barn swallow (Møller 1992) and some other species (e.g. McGraw et al. 2001; Pryke et al. 2001; Thusius et al. 2001) have also found a relationship between male ornament expression and timing of breeding.

Although our findings are in accordance with two of the mechanisms for sexual selection (timing of breeding and extra-pair mating), assumed to operate in socially monogamous species, we cannot infer a causal relationship between male ornamentation and sexual selection. Theoretically, this covariation between tail streamer length and fertilization success can be explained by an age effect, in which young and short-tailed males invest less in fertilization effort than older and longer-tailed males. If so, life history patterns can explain the observed correlations without any need to invoke sexual selection theory. We were unable to determine the age of adult barn swallows, but it is known that male tail streamer length in this species increases with age, mainly from the first to the second year of life (Møller 1994). Thus, the opportunity for sexual selection on tail streamer length is presumably less than indicated by the present result. Nevertheless, studies of the European barn swallow have shown that males with long tail streamers have a mating advantage even when the effect of age is controlled for statistically (Møller 1994; Møller and Tegelström 1997), and that the length of male tail streamers is a heritable character (Møller 1991). However, these assumptions need to be verified for the North American barn swallow before firm conclusions are drawn.

In the North American barn swallow, there is a higher frequency of individuals with chestnut-coloured ventral sides than in the European counterpart (Turner and Rose 1989; Møller 1994). A recent study claimed that the ventral colour, rather than the length of the tail streamers, is a sexually selected trait in North American barn swallows (Safran and McGraw 2004), thus suggesting geographic variation in sexual signalling in the barn swallow. Safran and McGraw (2004) used the number of fledged offspring as a measure of male reproductive success without analysing paternity, and thus, the realised fertilization success of males may have deviated largely from the apparent success (e.g. Yezerinac et al. 1995; Delhey et al. 2003; this study). Assessing paternity, both within-pair and extra-pair, is crucial for obtaining a good measure of male reproductive success.

In conclusion, our main findings are that extra-pair paternity significantly increased the variance in male fertilization success, thereby providing an opportunity for sexual selection. The tail streamer length was a significant predictor of a male's realised fertilization success, mainly mediated through a higher extra-pair success for males with long tail streamers. Thus, our results indicate a directional sexual selection on tail streamer length in the North American barn swallow.

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