

Male tail streamer length does not predict apparent or genetic reproductive success in North American barn swallows *Hirundo rustica erythrogaster*

Colby R. Neuman, Rebecca J. Safran and Irby J. Lovette

C. R. Neuman, R. J. Safran (correspondence) and I. J. Lovette, Evolutionary Biology Program, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Rd and Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14850. – Present address of R.J. Safran: Department of Ecology and Evolutionary Biology, 106A Guyot Hall, Princeton University, Princeton, New Jersey 08544. Email: rsafran@Princeton.EDU

In the socially monogamous barn swallow, previous studies of individuals in the European subspecies *Hirundo r. rustica* have shown that a male's tail streamer length is under strong sexual selection and is positively associated with several measures of reproductive success, including a low probability of being cuckolded by other males. The prominence of these results has led to subsequent experimental and correlational investigations of individuals in the phenotypically divergent subspecies *H. r. erythrogaster* in North America, where it has been shown that male tail streamer length is not as strongly associated with reproductive success as in European populations. We examined relationships between male tail streamer length and patterns of: (1) social mate selection and reproductive success, and (2) extra-pair paternity in 265 progeny of 53 social fathers within a New York barn swallow population. Although tail streamers in this population were sexually dimorphic, male tail streamer length did not predict patterns of mate selection, seasonal reproductive success, or extra-pair paternity. Moreover, in contrast to the strong positive relationships between paternity and male streamer length in European populations, summarized in this paper, we found no positive relationship between a male's paternity of young in the nest he is attending and his tail streamer length in our study population in New York. Our results further corroborate recent suggestions that the function of sexual signals varies geographically in this species, although we await additional experimental analyses on streamer lengths to understand the maintenance of sexual dimorphism in this trait.

Many species with socially monogamous mating systems display exaggerated ornaments that appear to be beyond their naturally selected optimum (Darwin 1859, 1871). Extra-pair matings are prevalent in many monogamous breeding systems; as such, many of these seemingly monogamous species are in fact not genetically monogamous. For example, a review by Griffith et al. (2002) found extra-pair matings in 75 out of the 99 socially monogamous species in which genetic paternity analyses had then been conducted. Extra-pair matings, and the possible reproductive skew that might result from them, are important to study because of their potential to contribution to sexual selection on ornamental traits. Thus, assaying genetic paternity is critical for determining whether or not extra-pair

fertilizations contribute to sexual selection on male traits in monogamous species (e.g., Webster et al. 1995, Byers et al. 2004, Whittingham and Dunn 2005). There is no consistent pattern between degree of male ornamentation and genetic paternity in studies of birds, (e.g., a positive correlation between male mask size and extra-pair paternity in common yellowthroats *Geothlypis trichas*, Thusius et al. 2001, no correlation between plumage color and extra-pair paternity in house finches *Carpodacus mexicanus*, Hill et al. 1994, reviewed in Griffith et al. 2002, Westneat and Stewart 2003). However, analyses that examine correlations between paternity and male ornaments among populations that possess variation in male phenotypes offer the potential to add important insights into whether differential

sexual selection within these populations maintains the variation in ornamentation between populations.

Tail streamers in the nominate European population of the barn swallow *Hirundo rustica rustica* have become a textbook example of a sexual selected trait (Møller 1988, 1994). Females prefer males with the longest tails and, among paired individuals, female tail length is positively correlated with male streamer length, providing evidence for assortative mating based on this trait (Møller 1993). Long-tailed males produce the most offspring (in their first clutches and total number of young per season) each year because they pair and breed earlier and successfully fledge more broods than shorter-tailed males (Møller 1988, 1994). Experimental manipulations of tail streamers corroborate the link between male tail streamer lengths and both within-pair and extra-pair paternity (Møller and Tegelström 1997, Saino et al. 1997), demonstrating that streamer length in this population of barn swallows is under strong contemporary sexual selection.

Intriguing phenotypic differences exist among the six subspecies of barn swallows (Cramp 1988). Swallows from the North American populations are substantially more colorful throughout the ventral region and have shorter tail streamers compared to individuals in European populations (Cramp 1988). Recently, Safran and McGraw (2004) found that ventral coloration, but not streamer lengths, is correlated with patterns of pairing and seasonal reproductive success in a population of North American barn swallows, and experimental manipulations of male coloration demonstrates that individuals use this trait to assess male quality (Safran et al. 2005). Previous correlational studies of North American populations have not found the positive relationships between male tail streamer lengths and measures of seasonal reproductive success that are typical of males in European populations, which may indicate the lack of strong sexual selection on this trait in this continental population (Smith and Montgomerie 1991, Briceno 2002, but see Kleven et al. 2006). The one study that experimentally manipulated streamer lengths in the North American population yielded equivocal results, in part because sample sizes for the streamer length treatments were very small and the experiment included no control treatment (Smith et al. 1991).

Previous studies suggest that extra-pair matings are a prevalent reproductive strategy in barn swallows both in Europe and North America. Extra-pair offspring have been detected in all previous studies of the genetic mating system of *H. rustica rustica* in Europe (Smith et al. 1991, Møller and Tegelström 1997, Saino et al. 1997), as well as in two studies conducted in the same North American population of barn swallows (Smith et al. 1991, Kleven et al. 2006). Moreover, the 19 investigations of the genetic mating systems of other Hirundinidae species show that extra-pair matings

appear to be widespread in the swallow family as a whole (Barber et al. 1996, 1998, Barber and Robertson 1999, Conrad et al. 2001, Dunn and Robertson 1993, Dunn et al. 1994a,b, Kempenaers et al. 1999, Magrath and Elgar 1997, Moore et al. 1999, Morton et al. 1990, Riley et al. 1995, Wagner et al. 1996a,b, 1997, Whittingham and Liffield 1995a,b, Whittingham and Dunn 2001, Whittingham et al. 2003). In combination, these studies suggest that extra-pair paternity is a common component of swallow mating systems, as the population-level frequency (pooling broods) of extra-pair young in hirundinids ranges between 15% in the mangrove swallow (Moore et al. 1999) to as much as 53% in the tree swallow (Dunn et al. 1994b).

In this study, we examined a breeding population of North American barn swallows to determine whether tail streamer length predicts a male's apparent (number of fledged young in his nest) and genetic (paternity of those young) reproductive success. Based on the general findings from other studies of North American barn swallows, (Smith and Montgomerie 1991, Smith et al. 1991, Briceno 2002, Safran and McGraw 2004), we predicted that natural variation in male tail streamer lengths would not explain variation in measures of seasonal reproductive success, patterns of pairing, and paternity.

Methods

Field methods

We studied a population of barn swallows at 22 breeding sites in Tompkins County, New York from May-August 2002. Using mist nets, we captured swallows during the first two weeks of the breeding season. We uniquely marked individuals with enamel-based paints following methods used by Shields and Crook (1987) and numbered aluminum rings for later identification. At sites where individuals were captured in previous years, we were able to obtain approximate age information based on the number of years an individual was observed in our study area. We checked nests daily to determine breeding onset (Julian date on which first egg was laid), number of nesting attempts (1 or 2), and annual reproductive success (total number of young fledged within the season), and we identified pairs as they constructed nests, incubated eggs, and fed nestlings.

At capture, we also measured the length of both the right and left tail streamer of adult birds to the nearest 0.5 mm with a ruler (Smith et al. 1991). To assess the degree of measurement error, we measured each streamer three times. The separate measurements of streamers were highly repeatable (repeatability = 0.99, $F_{19,39} = 304.31$, $P < 0.001$; Lessells and Boag 1987). For

statistical comparisons of tail-streamer length, we used measures from the right side of both males and females (Smith and Montgomerie 1991) to avoid the problem of using the average of right and left sides in cases where streamer lengths were asymmetric. A blood sample was collected from each bird and stored in lysis buffer until later use (Seutin et al. 1991, Hoelzel, 1992). We omitted all birds with broken or missing tail streamers from our sample ($N = 7$ females and 7 males; Shyoff and Møller, 1999). Thirty of the pairs in this study were part of an experiment that was conducted after their first clutch of eggs were laid. Because the first clutches were collected as part of the experimental protocol, DNA for the paternity analyses was extracted from embryos, whereas DNA was extracted from the blood of nestlings for the remaining 31 pairs in this study.

Because of experimental manipulations between first and second breeding attempts in some of the pairs in our study population, we do not include data on second broods in this paper.

Lab methods

We used three polymorphic microsatellite loci for genetic parentage analyses: HrU6, HrU7 (Primmer et al. 1995), and HrU10 (Primmer et al. 1996), two of which are hyper-variable in this and other populations of barn swallows (Saino et al. 1997, Brohede et al. 2002). Molecular analyses follow detailed information provided in Safran et al. (2005).

Paternity exclusion

We used Genemapper version 3.0, software, (Applied Biosystems) to determine allele sizes and assign genotypes for each individual at the three loci. We used CERVUS, version 2.0 to calculate the exclusion probabilities for assessing parentage, and to test for the presence of null alleles (Marshall et al. 1998). To conduct paternity exclusions we conservatively defined a nestling with two or more (vs. just one) mismatches with the social male as an extra-pair young to help avoid false exclusions arising from null alleles at single loci (Dakin and Avise 2004). Because of well documented single repeat mutations at HrU6 and HrU10 (Brohede et al. 2002), we did not exclude the social male as the genetic father of a given offspring if the alleles mismatched by only 2 base pairs. In a larger data set from individuals in our study area, mismatch of one to two base pairs only occurred 8 times in 419 social parent-offspring comparisons (1.91%), and only at HrU10. The majority of these eight 2-bp mismatches between parents and offspring likely involve mutations, as Brohede et al. (2002) reported a similar mutation rate of 1.56% for HrU10.

Statistical analyses

In some cases, our data did not conform to the assumptions of parametric analyses (linearity or normality). When linear regression was not possible, we used nonparametric tests to examine relationships between tail streamers and measures of reproductive performance. We examined differences between males and females in the variability of tail streamers using two sample tests for variance (Neter et al. 1996). In the case of two-group analyses where variances are unequal, we used the approximate t computation for unequal variances using SAS PROC TTEST. The degrees of freedom for the approximate t computation are based on Satterthwaite's approximation (SAS Institute 1990).

We applied a logistic model using the binomial independent variable (number of own young in clutch/total number of young in clutch) and a logit-link function to analyze the relationship between within-pair paternity and male streamer length.

To facilitate comparisons with European studies of barn swallows, we also performed the same analyses as reported in Møller et al. (1998, Fig. 1a), Saino et al. (1997, Fig. 3), Møller and Tegelström (1997, Fig. 1), and Møller (1992, Tables 1 and 2).

Tests are two-tailed and $\alpha = 0.05$ in all cases. Sample sizes vary slightly among comparisons due to the exclusion of individuals having either frayed or missing tail streamers from tests involving that trait and the deletion of families for whom we lacked the genotypes of both parents. All analyses were performed using SAS (version 9.1).

Results

Sample sizes

Blood samples were collected and DNA was subsequently extracted for all 61 (61 males and 61 females)

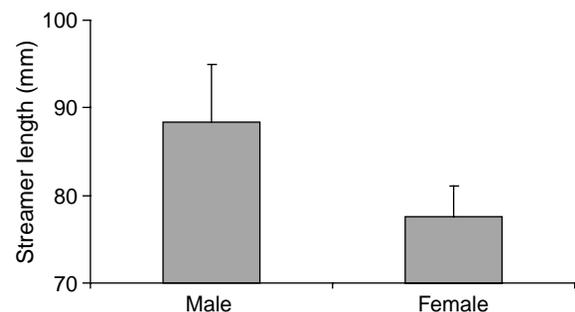


Fig. 1. Tail streamer lengths are sexually dimorphic in our study population in central New York. Male tail streamers ($N = 54$) were significantly longer and more variable than female tail streamers ($N = 54$). Histograms portray means and one standard deviation.

Table 1. Variability of microsatellite loci in 59 complete barn swallow families, with additional data from replacement clutches from first breeding attempts for 30 pairs. P_e is the probability of exclusion based on variability at a single locus; h_e is the expected heterozygosity and h_o is the observed heterozygosity. The total probability of paternal exclusion using all three loci is 0.997.

Locus	No. of alleles	P_e	h_e	h_o	Null frequency
HrU6	70	0.96	0.96	0.92	0.005
HrU7	3	0.26	0.50	0.47	0.02
HrU10	95	0.92	0.98	0.95	0.03

pairs of barn swallows studied. Eight of these families were excluded from our analyses due to extraction or amplification problems. The 53 pairs studied produced a total of 265 eggs/nestlings in their first breeding attempts with a mean (\pm standard deviation) clutch size of 5.0 ± 0.65 (range 3–6) in their first brood. Due to the occurrence of broken tail streamer lengths for families with complete paternity data, the total sample size for the analysis between paternity and tail streamer length is 46 pairs.

Microsatellite genotyping

Two of the three microsatellite markers (HrU6 and HrU10) had high allelic diversity and were extremely variable, as found previously in studies of other *Hirundo* populations (Primmer et al. 1996, Saino et al. 1997, Brohede et al. 2002). Even considered singly, each of these markers gave high probabilities of exclusion (Table 1). Most paternal exclusion studies use a larger number of less variable microsatellite markers, but our three markers gave us high power to exclude social males as the sires of extra-pair offspring. For HrU6, the 70 alleles present in our population had an observed heterozygosity of 0.92, giving a 0.96 probability of exclusion. For HrU10, the 96 alleles had an

observed heterozygosity of 0.95, generating an exclusion probability of 0.92. For HrU7, the 3 alleles present in our population had an observed heterozygosity of 0.47, producing a probability of exclusion of 0.26. Comparisons of observed heterozygosities and predicted heterozygosities suggest that null alleles may be present at all three loci, but at low frequencies (Table 1). Simulation studies by Dakin and Avise (2004) indicate rare null alleles ($P < 0.20$) would create a slight underestimate of the average exclusion probability at a locus, therefore these rare null alleles (if present) are unlikely to cause strong biases in our parentage analyses. When all markers were considered simultaneously, our total probability of paternal exclusion was 0.997.

Streamer variation

In our study population, the tail streamers of male barn swallows were longer and more variable ($N = 54$, mean \pm SD = 86.74 ± 8.32 mm) than the streamers of females ($N = 54$, mean \pm SD = 77.28 ± 3.67 mm; two-sample t-test for unequal variance, $t = 9.74$, $df = 68.41$, $P < 0.0001$, direct comparisons of 46 pairs individuals with intact streamers; two-sample test for variances, $F = 3.56$, $df = 45$, $P < 0.001$; Fig. 1). When comparing mates to one another, we found no significant relationship between male tail streamer length and female tail streamer length, suggesting that mating is not positively assortative with respect to tail streamer length (linear regression $F_{1,45} = 0.02$, $P > 0.89$; Fig. 2).

Patterns of paternity

Extra-pair paternity was prevalent in the population studied. Nearly half of the broods (26 of 53) contained at least one extra-pair offspring. The mean proportion of extra-pair young per first brood was 0.23 ± 0.30 .

Table 2. Comparisons of reproductive parameters as a function of male streamer length in European studies and our study population in Ithaca, New York. F , and P , and n are values for the variable 'streamer length' in ANCOVA models that also statistically correct for age and annual variation. NP indicates the F statistic for the 'streamer length' is not provided in Møller 1992. NS indicates the variable is not statistically significant. *P-full model* indicates the significance of the entire ANCOVA model, and letters indicate the significance of the additional variable (age) in the full model as follows: The effect of individual age is not (A) or is (B) significant in the model.

Variable	Study area	Streamer length	N	F	P-variable	P- Full model	Source
Brood size at fledging (1st clutch)	Kraghede, Denmark	0.03	261	NP	<0.05	<0.001A	Møller, 1992 Table 2
Julian lay date		-0.34	261	NP	<0.001	<0.0001 A	Møller, 1992 Table 1
Total no. of fledglings		0.05	281	NP	<0.01	<0.05 B	Møller, 1992 Table 2
Brood size at fledging (1st clutch)	Ithaca, New York	0.02	237	2.68	NS	<0.05 B	Safran, unpubl. data
Julian lay date		0.08	232	10.77	<0.001	<0.001 B	Safran, unpubl. data
Total no. of fledglings		0.04	246	10.57	NS	<0.001 B	Safran, unpubl. data

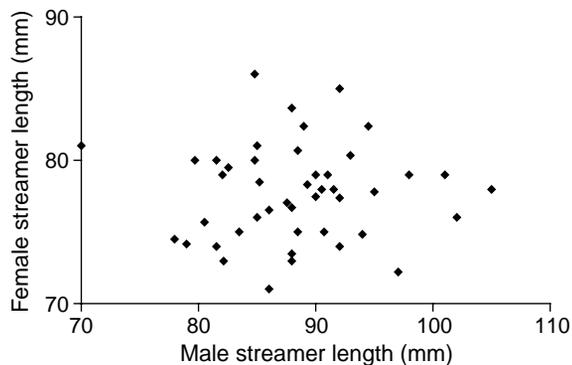


Fig. 2. We found no positive correspondence between male and female tails streamer length and thus, no evidence of positive assortative mating with respect to this trait in our study population, $N = 46$ breeding pairs.

Julian lay date did not predict patterns of paternity (Spearman rank, $R_s = -0.07$, $P > 0.62$, $N = 52$), nor were older males (first year breeders vs. not first year breeders) more likely to have more paternity (two-sample t -test, $t = -0.32$, $P > 0.74$, $df = 50$), as has been reported in other studies (Griffith et al. 2002). As part of another study, we found no significant differences in the rate of extra-pair matings and group size (measured as the number of pairs nesting in the same or adjacent structures), suggesting that breeding density does not affect reproductive strategies in this population (Safran 2005), thus it was not necessary to statistically control for group size.

Streamer length and fitness correlates

Male tail streamer length did not correlate with the clutch initiation date of his social mate (Spearman rank, $R_s = -0.14$, $P > 0.33$; $N = 51$, Fig. 3a), or the clutch size (first brood) produced in the nest he was associated with ($R_s = 0.16$, $P > 0.23$; $N = 53$, Fig. 3b). In contrast to patterns typical of populations in Europe, a male's tail streamer length did not predict his paternity contribution to the young in his social nest (Binomial test: $\chi^2 = 1.97$, $P > 0.15$, $N = 46$, parameter estimate own young: total young in first brood = $-0.05 + 0.04$, Fig. 4).

Comparisons with European studies

Table 2 portrays differences in correlations between reproductive parameters and male streamer lengths between our study population and one of the most intensively studied populations in Europe.

Other paternity studies of barn swallows in Europe report results that contrast with our findings. For example, Saino et al. (1997) report a significant positive

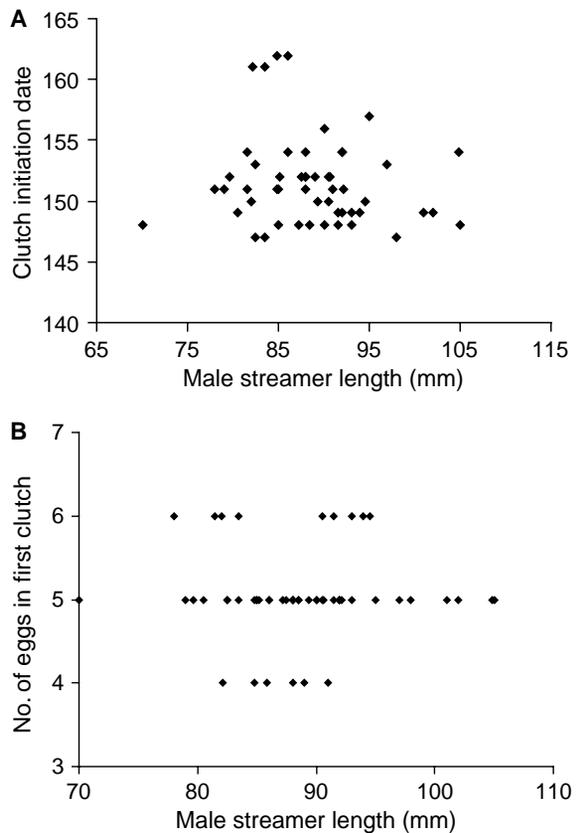


Fig. 3. A) Male tail streamer length did not significantly relate to the clutch initiation date of his mate, $N = 51$ pairs; B) Male tail streamer length did not predict the number of eggs produced in the first nest he attended, $N = 53$ pairs.

association between streamer length and the proportion of offspring sired in first breeding attempts in a northern Italian population of barn swallows (Kendall

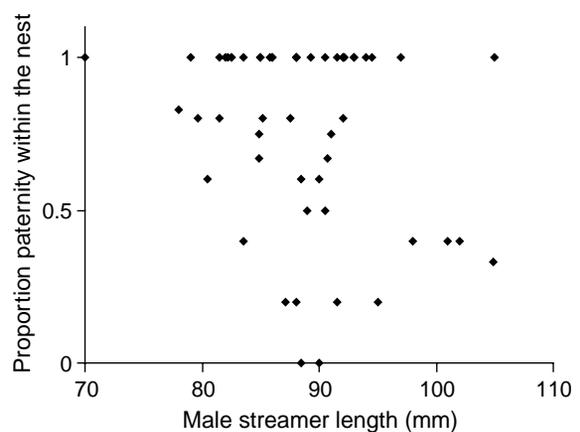


Fig. 4. A male's tail streamer length is not associated with the probability of caring for his own young in the nest he attended ($N = 46$ pairs).

Tau = 0.29, $P < 0.005$, $N = 52$, Fig. 3 in Saino et al. 1997), whereas we found no association between these two variables using the same test statistic (Kendall Tau = -0.14 , $P > 0.19$, $N = 46$). Likewise, Møller and colleagues (1998) report a significant linear relationship between the proportion of offspring sired by the resident male of the nest in relation to his streamer length from a population near Milan, Italy ($F_{1,24} = 5.91$ $P = 0.023$, parameter estimate for tail length = 0.019, SE = 0.008), whereas we found no association between these two variables in males from Ithaca, New York using the same analyses ($F_{1,46} = 2.79$ $P > 0.10$, parameter estimate for tail length = -0.011 , SE = 0.006). Similarly, Møller and Tegelström (1997) also report a negative correspondence between the proportion of broods being sired by extra-pair males and the streamer length of the male nest owner in a population in Denmark, indicating that longer-tailed males are less likely to be cuckolded (Kendall Tau = -0.35 , $P < 0.001$, $N = 47$; Fig. 1). However, using the same analyses, we found no such correspondence between a male's streamer length and his probability of being cuckolded (Kendall Tau = 0.11 $P > 0.27$, $N = 53$).

Discussion

Sexually selected traits are often sexually dimorphic, predict patterns in mate selection, and show a relationship with various measures of reproductive success (Andersson 1994). In this study, we examined patterns of reproductive success, including extra-pair paternity in relation to male tail streamer lengths in a North American population of the barn swallow. Although tail streamers were sexually dimorphic, we found no significant positive relationship between male tail streamer length and measures of seasonal reproductive success, including within-pair paternity, suggesting that sexual selection is significantly reduced on the tail streamers of male barn swallows in our study area.

In our study of genetic paternity in North American barn swallows, we found no significant statistical relationship between male streamer length and the paternity of young in his nest. This lack of a strong relationship between male streamer length and genetic paternity in New York differs from similar correlational analyses of males in a European population where tail streamer length strongly predicted patterns of extra-pair paternity (Saino et al. 1997, Møller et al. 1998). Thus, our results, along with an experimental study of extra-pair paternity conducted in Ontario (Smith et al. 1991), suggest that sexual selection on male tail streamer length is at least strongly reduced, if not absent, in the North American population. Interestingly, a recent analysis of both within- and extra-pair

components of paternity suggest that long-streamered barn swallows males from four colonies in Ontario, Canada received extra-pair benefits from females outside their social pair bond, but not within-pair benefits from their own mates, compared to their shorter-streamered neighbors (Kleven et al. 2006).

Potential caveats

One potential caveat of our results is that we did not perform parentage assignment analyses. This was primarily because in order to avoid site and colony size effects, we sampled across a large number of different breeding locations, and hence the number of potential extra-pair sires was very large (a total of 155 males bred at these locations, additional males bred at nearby non-monitored locations, and the population includes males that remain unpaired throughout the breeding season; Safran, unpublished data). This lack of information on the identity of males fathering extra-pair young could bias our interpretation if longer-tailed males had a higher likelihood of paternity via extra-pair copulations. We cannot test this possibility with the present microsatellite data, but previous studies of European barn swallows in which parentage assignments were conducted have shown that a male's rate of within-pair paternity is predictive of, and consistent with, his rate of extra-pair paternity (Møller and Tegelström 1997, Saino et al. 1997). If females distribute paternity based on phenotypic cues, such as tail streamers, males with longer tail streamers are unlikely to have elevated paternity of extra-pair young in our population.

Second, although our data are correlational and not based on experiments, results from correlational and experimental paternity studies have repeatedly corroborated one another in both North American and European populations of the barn swallow (Smith et al. 1991; Møller and Tegelström 1997; Saino et al. 1997). In Europe, both correlational and experimental studies demonstrate reproductive advantages for males with long streamers.

Finally, another potential caveat is that poor weather reduced variation in the first lay dates of pairs which is an important predictor of seasonal reproductive success (Safran and McGraw 2004). However, data from other years of our study long-term also reveal no statistically significant relationship between male streamer length and correlates of seasonal reproductive success, removing the possibility that the data presented from 2002 in this study are confounded by weather patterns (Safran and McGraw 2004, and data summarized in Table 2 of this paper).

Explanations for geographic variation in tail streamers

Interestingly, despite similar sample sizes and similar parameter estimates for at least two of the three variables compared in Table 2 of this paper, variation in male streamer length does not significantly explain variation in measures of seasonal reproductive success in four successive breeding seasons in central New York, in striking contrast to the findings of other studies in Europe (e.g., Møller 1992, Møller 1994). Despite similar parameter estimates for the effects of streamer length on brood size and the total number of fledglings produced in a breeding season in Denmark and central New York (Table 2), it is worth noting that these estimates are all very low (all ≤ 0.05) indicating at most a small effect of this variable for explaining variation in these two measures of seasonal reproductive performance. Additionally, whereas male age explains variation in patterns of reproductive performance in our study population in New York, this variable is not statistically significant in the analyses reported by Møller et al. (1992); Tables 1 and 2), suggesting different correlates of seasonal reproductive performance within the geographically isolated populations. Although these analyses are only indirect comparisons vs. the direct analysis of data from the different study areas in one model, they do corroborate the mounting evidence that the function of elongated streamers varies between European and North American populations (e.g., Smith et al. 1991, Briceno 2002, Safran and McGraw 2004, but see Kleven et al. 2006).

Similar genetic methods, including at least one microsatellite marker in common (HrU6) were employed in 3 of the four paternity studies summarized here with the exception of Møller and Tegelström (1997) who used DNA fingerprinting to assay genetic paternity. Like this study, Saino et al. (1997) report data for first broods only, whereas the other two studies cited here (Møller and Tegelström 1997, Møller et al. 1998) apparently report paternity rates on young combined from first and second broods. However, these comparisons should not be confounded by the number of broods analyzed in each study, as paternity rates were found to be highly repeatable between first and second broods (Møller and Tegelström 1997).

Interestingly, despite latitudinal variation in streamer lengths in European populations (Møller 1995) where males in Denmark have longer streamers compared to males in Italy, the function of streamers, in terms of the associated benefits of social and genetic reproductive success, do not vary tremendously between these two intra-continental populations (Møller and Tegelström 1997, Saino et al. 1997, Møller et al. 1998). Although the breeding latitude of males in our study area most closely corresponds to males in the Italian study areas

vs. males in Denmark, we detected no similarities in the benefits associated with elongated streamers in our population in New York as compared to males in the intensively studied population near Milan where benefits associated with this sexual signal are apparent. Long term data sets and genetic paternity analyses from populations in southern Europe may, however, demonstrate results more similar to our own from central New York.

Considered in concert, the results of this study and others conducted in North America (Smith et al. 1991, Briceno 2002, Safran and McGraw 2004) suggest that the pattern of sexual selection on tail streamers varies geographically. Smith and Montgomerie (1991) have suggested that this geographic variation may be related to differences in male behavior during the incubation period, as male barn swallows in North America spend approximately 12% of daylight hours on the nest during the incubation stage of the breeding cycle (Ball 1983, Smith and Montgomerie 1992), whereas males in the European population do not participate in incubation (Møller 1994). In this case, it is possible that the longer-tailed males in North America may be at a higher risk of tail streamer breakage during incubation at nests where streamers often brush against a wall or roof. The resulting broken streamers may be shorter than the aerodynamic optimum, thereby decreasing the fitness of the bird (Smith and Montgomerie 1991). This explanation isn't compelling because the average length of male streamers in North America is equivalent to those of females in Europe. Another potential explanation is that males in North America have less time to forage due to their incubation duties, and therefore must be more efficient flyers (Smith and Montgomerie 1991); the additional time constraint of incubation may be sufficient enough to select against those individuals whose tails are beyond the aerodynamic optimum (Evans 1998, Buchanan and Evans, 2000, Rowe et al. 2001). Consistent with this explanation, previous studies have found that only a small distal region of the tail streamer (approximately 10–15 mm) in the European population appears to be under sexual selection, while the majority of the tail streamer length has evolved to a naturally selected optimum (Evans, 1998, Buchanan and Evans, 2000, Rowe et al. 2001) that is very similar to the shorter mean streamer length in the North American population (Cramp 1988).

Because male ventral coloration predicts patterns in the onset of breeding in females, the ability to produce multiple broods and overall reproductive success (Safran and McGraw 2004), in addition to being causally related to a male's paternity (Safran et al. 2005), feather coloration may be a more reliable signal of male quality than tail streamer length in our North American population. The data presented here further support these findings.

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References

- Andersson, M. 1994. Sexual selection. – Princeton University Press, Princeton.
- Ball, G. F. 1983. Functional incubation in male barn swallows. – *Auk* 100: 998–1000.
- Barber, C. A., Robertson, R. J. and Boag, P. T. 1996. The high frequency of extra-pair paternity in tree swallows is not an artifact of nestboxes. – *Behav. Ecol. Sociobiol.* 38: 425–430.
- Barber, C. A., Robertson, R. J. and Boag, P. T. 1998. Experimental mate replacement does not increase extra-pair paternity in tree swallows. – *Proc. R. Soc. B* 265: 2187–2190.
- Barber, C. A. and Robertson, R. J. 1999. Floater males engage in extrapair copulations with resident female tree swallows. – *Auk* 116: 164–169.
- Briceno, A. T. 2002. Tail length and sexual selection in the North American barn swallow *Hirundo rustica erythrogastrer*. – University of Tulsa, Tulsa.
- Brohede, J., Primmer, C. R., Møller, A. and Ellegren, H. 2002. Heterogeneity in the rate and pattern of germline mutation at individual microsatellite loci. – *Nucl. Acids Res.* 30: 1997–2003.
- Buchanan, K. L. and Evans, M. R. 2000. The effect of tail streamer length on aerodynamic performance in the barn swallow. – *Behav. Ecol.* 11: 228–238.
- Byers, B. E., Mays, H. L., Stewart, I. R. K. and Westneat, D. F. 2004. Extrapair paternity increases variability in male reproductive success in the chestnut-sided warbler (*Dendroica pensylvanica*), a socially monogamous songbird. – *Auk* 121: 788–795.
- Conrad, K. F., Johnston, P. V., Crossman, C., Kempnaers, B., Robertson, R. J., Wheelwright, N. T. and Boag, P. T. 2001. High levels of extra-pair paternity in an isolated, low density, island population of tree swallows (*Tachycineta bicolor*). – *Mol. Ecol.* 10: 1301–1308.
- Cramp, S. 1988. Birds of the western Palearctic, vol. 5. – Oxford Univ. Press, Oxford.
- Dakin, E. E. and Avise, J. C. 2004. Microsatellite null alleles in parentage analysis. – *Heredity* 93: 504–509.
- Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. – John Murray, London.
- Darwin, C. 1871. The descent of man, and selection in relation to sex. – John Murray, London.
- Dunn, P. O. and Robertson, R. J. 1993. Extra-pair paternity in polygynous tree swallows. – *Anim. Behav.* 45: 231–239.
- Dunn, P. O., Whittingham, L. A., Lifjeld, J. T., Robertson, R. J. and Boag, P. T. 1994a. Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. – *Behav. Ecol.* 5: 123–129.
- Dunn, P. O., Robertson, R. J., Michaud-Freeman, D. and Boag, P. T. 1994b. Extra-pair paternity in tree swallows: why do females mate with more than one male? – *Behav. Ecol. Sociobiol.* 35: 273–281.
- Evans, M. R. 1998. Selection on swallow tail streamers. – *Nat. London* 394: 233–234.
- Griffith, S. C., Owens, I. P. F. and Thuman, K. A. 2002. Extra-pair paternity in birds: a review of interspecific variation and adaptive function. – *Mol. Ecol.* 11: 2195–2212.
- Hill, G. E., Montgomerie, R., Roeder, C. and Boag, P. T. 1994. Sexual selection and cuckoldry in a monogamous songbird-implications for sexual selection theory. – *Behav. Ecol. Sociobiol.* 35: 193–199.
- Hoelzel, A. R. ed. 1992. Molecular genetic analysis of populations: a practical approach. – IRL Press at Oxford Univ. Press, Oxford.
- Kempnaers, B., Congdon, B., Boag, P. and Robertson, R. J. 1999. Extrapair paternity and egg hatchability in tree swallows: evidence for the genetic compatibility hypothesis? – *Behav. Ecol.* 10: 304–311.
- Kleven, O., Jacobsen, F., Izadnegahdar, R., Robertson, R. J. and Lifjeld, J. T. 2006. Male tail streamer length predicts fertilization success in the North American barn swallow (*Hirundo rustica erythrogastrer*). – *Behav. Ecol. Sociobiol.* 59: 412–418.
- Lessells, C. M. and Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. – *Auk* 104: 116–121.
- Magrath, M. J. L. and Elgar, M. A. 1997. Paternal care declines with increased opportunity for extra-pair matings in fairy martins. – *Proc. R. Soc. B* 264: 1731–1736.
- Marshall, T. C., Slate, J., Kruuk, L. E. B. and Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. – *Mol. Ecol.* 7: 639–655.
- Møller, A. P. 1988. Female choice selects for male sexual tail ornaments in the monogamous swallow. – *Nature*. 332: 640–642.
- Møller, A. P. 1992. Sexual selection in the monogamous barn swallow (*Hirundo rustica*). II. Mechanisms of sexual selection. – *J. Evol. Biol.* 5: 603–624.
- Møller, A. P. 1993. Sexual selection in the barn swallow *Hirundo rustica*. III. Female tail ornaments. – *Evolution* 47: 417–431.
- 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. – *J. Evol. Biol.* 8: 3–19.
- Møller, A. P., Saino, N., Taramino, G., Galoetti, P. and Ferrario, S. 1998. Paternity and multiple signaling: effects of a secondary sexual character and song on paternity in the barn swallow. – *Am Nat.* 151: 236–242.

- Møller, A. P. and Tegelström, H. 1997. Extra-pair paternity and tail ornamentation in the barn swallow *Hirundo rustica*. – Behav. Ecol. Sociobiol. 41: 353–360.
- Moore, O. R., Stutchbury, B. J. M. and Quinn, J. S. 1999. Extrapair mating system of an asynchronously breeding tropical songbird: the mangrove swallow. – Auk 116: 1039–1046.
- Morton, E. S., Forman, L. and Braun, M. 1990. Extrapair fertilizations and the evolution of colonial breeding in purple martins. – Auk 107: 275–283.
- Neter, J., Kutner, M. H., Nachtsheim, C. J., and Wasserman, W. 1996. Applied linear statistical models, 4th ed. – Irwin, Chicago.
- Primmer, C. R., Møller, A. P. and Ellegren, H. 1995. Resolving genetic relationships with microsatellite markers: a parentage testing system for the swallow *Hirundo rustica*. – Mol. Ecol. 4: 493–498.
- Primmer, C. R., Møller, A. P. and Ellegren, H. 1996. New microsatellites from the pied flycatcher *Ficedula hypoleuca* and the swallow *Hirundo rustica*. – Hereditas 124: 281–283.
- Riley, H. T., Bryant, D. M., Carter, R. E. and Parkin, D. T. 1995. Extra-pair fertilizations and paternity defence in house martins, *Delichon urbica*. – Anim. Behav. 49: 495–509.
- Rowe, L. V., Evans, M. R. and Buchanan, K. L. 2001. The function and evolution of the tail streamer in hirundines. – Behav. Ecol. 12: 157–163.
- Safran, R.J. 2005. From individuals to populations: female habitat- and mate-selection decisions and group size variation in barn swallows. – Cornell University, Ithaca.
- Safran, R. J. and McGraw, K. J. 2004. Plumage coloration, not length or symmetry of tail-streamers, is a sexually selected trait in North American barn swallows. – Behav. Ecol. 15: 455–461.
- Safran, R. J., Neuman, C. R., McGraw, K. J. and Lovette, I. J. 2005. Dynamic paternity allocation as a function of male color in barn swallows. – Science 309: 2210–2212.
- Saino, N., Primmer, C. R., Ellegren, H. and Møller, A. P. 1997. An experimental study of paternity and tail ornamentation in the barn swallow (*Hirundo rustica*). – Evolution 51: 562–570.
- SAS Institute Inc. 1990 SAS/STAT User's Guide, version 6, 4th ed., vol. 2. – SAS Institute Inc., Cary.
- Seutin, G., White, B. N. and Boag, P. T. 1991. Preservation of avian blood and tissue samples for DNA analyses. – Can. J. Zool. 69: 82–90.
- Shields, W. M. and Crook, J. R. 1987. Barn swallows coloniality: a net cost for group breeding in the Adirondacks? – Ecology 68: 1373–1386.
- Shykoff, J. A. and Møller, A. P. 1999. Fitness and asymmetry under different environmental conditions in the barn swallow. – Oikos 86: 152–158.
- Smith, H. G. and Montgomerie, R. 1991. Sexual selection and tail ornaments of North American barn swallows. – Behav. Ecol. Sociobiol. 28: 195–201.
- Smith, H. G., Montgomerie, R., Pöldmaa, T., White, B. N. and Boag, P. T. 1991. DNA fingerprinting reveals relation between tail ornaments and cuckoldry in barn swallows, *Hirundo rustica*. – Behav. Ecol. 2: 90–98.
- Smith, H. G. and Montgomerie, R. 1992. Male incubation in barn swallows: the influence of nest temperature and sexual selection. – Condor 94: 750–759.
- Thusius, K. J., Peterson, K. A., Dunn, P. O. and Whittingham, L. A. 2001. Male mask size is correlated with mating success in the common yellowthroat. – Anim. Behav. 62: 435–446.
- Wagner, R. H., Schug, M. D. and Morton, E. S. 1996a. Confidence of paternity, actual paternity, and parental effort by purple martins. – Anim. Behav. 52: 123–132.
- Wagner, R. H., Schug, M. D. and Morton, E. S. 1996b. Condition-dependent control of paternity by female purple martins: implications for coloniality. – Behav. Ecol. Sociobiol. 38: 379–389.
- Wagner, R. H., Davidar, P., Schug, M. D. and Morton, E. S. 1997. Do blood parasites affect paternity, provisioning and mate-guarding in Purple Martins. – Condor 99: 520–523.
- Webster, M. S., Pruett-Jones, S., Westneat, D. F. and Arnold, S. J. 1995. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. – Evolution 49: 1147–1157.
- Westneat, D. F. and Stewart, I. R. K. 2003. Extra-pair paternity in birds: causes, correlates, and conflicts. – Annu. Rev. Ecol. Evol. Syst. 34: 365–396.
- Whittingham, L. A. and Dunn, P. O. 2001. Survival of extrapair and within-pair young in tree swallows. – Behav. Ecol. 12: 496–500.
- Whittingham, L. A., Dunn, P. O. and Clotfelter, E. D. 2003. Parental allocation of food to nestling tree swallows: the influence of nestling behaviour, sex and paternity. – Anim. Behav. 65: 1203–1210.
- Whittingham, L. A. and Dunn, P. O. 2005. Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds. – Behav. Ecol. 16: 138–144.
- Whittingham, L. A. and Lifjeld, J. T. 1995a. Extra-pair fertilizations increase the opportunity for sexual selection in the monogamous house martin *Delichon urbica*. – J. Avian Biol. 26: 283–288.
- Whittingham, L. A. and Lifjeld, J. T. 1995b. High paternal investment in unrelated young: extra-pair paternity and male parental care in house martins. – Behav. Ecol. Sociobiol. 37: 103–108.