



# Plumage brightness and age predict extrapair fertilization success of male tree swallows, *Tachycineta bicolor*

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In socially monogamous passerines, extrapair paternity can increase the variance in male reproductive success. If gaining extrapair fertilizations is linked to specific secondary sexual ornaments, the opportunity for sexual selection is enhanced. Therefore, to understand the evolution of male phenotypic characteristics, it is important to identify traits that predict male extrapair mating success. Tree swallows show among the highest rates of extrapair paternity known to occur in birds, yet it is unclear whether male extrapair mating success is associated with phenotypic traits that honestly advertise individual quality. We compared morphological characteristics and plumage coloration of male tree swallows that sired extrapair offspring with those that sired only within-pair offspring in the same breeding population to identify the characteristics that predict extrapair fertilization success. Males who produced extrapair offspring had brighter plumage, and were more likely to be returning breeders, than males that did not have extrapair young. In paired comparisons, however, there was no difference between extrapair males and the male they cuckolded. These results suggest that female tree swallows may prefer brighter or older individuals as extrapair mates, but also, that older males may invest more energy in pursuing extrapair copulations. Furthermore, since females had extrapair offspring in their nest regardless of their social mate's morphometric or plumage attributes, we suggest that extrapair mating may be a reproductive strategy allowing females to increase the genetic diversity, while maintaining genetic quality, of their offspring.

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Extrapair paternity is common in birds, including socially monogamous species (reviewed in Griffith et al. 2002). For females, multiple mating can enhance fertilization success or genetic quality of offspring, circumventing the constraints associated with strict monogamy (Petrie & Kempenaers 1998). For males, extrapair fertilizations may increase the total number of offspring they sire, improving their reproductive success. If all males are not equally successful in securing extrapair fertilizations, and phenotypic characteristics of males predict extrapair fertilization success, breeding outside the pair bond has the potential to increase the variance in male reproductive success and, in turn, increase the opportunity for sexual selection. Indeed, characteristics of males, including age (Richardson & Burke 1999), body condition

(Møller et al. 2003) and plumage quality (Delhey et al. 2003; Doucet et al. 2005), have been found to influence extrapair fertilization success in a number of species. Moreover, males that are successful at securing extrapair fertilizations may also lose less paternity in their own nests (Saino et al. 1997). Consequently, variance in male reproductive success, and thus the strength of sexual selection, may be significantly influenced by within-pair as well as extrapair fertilizations (Webster et al. 1995). In many species, there is no evidence for phenotypic differences between extrapair sires and the males they cuckold (e.g. Charmantier et al. 2004), and in some cases, extrapair sires are as likely to lose paternity in their own nests as are other males in the population (Yezerinac et al. 1995). Under these conditions, realized within-pair reproductive success of males appears to be unrelated to their phenotypic characteristics, and differential extrapair fertilization success may be particularly important in determining the strength of sexual selection.

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Tree swallows, *Tachycineta bicolor*, are socially monogamous passerines that show high levels of extrapair paternity: up to 90% of broods contain extrapair offspring, and between 35% and 69% of nestlings are sired by extrapair males (Lifjeld et al. 1993; Barber et al. 1996; Whittingham & Dunn 2001; O'Brien & Dawson 2007). The phenotypic quality of male tree swallows does not appear to influence their within-pair fertilization success (Barber et al. 1998), and this may indicate that the benefits of extrapair paternity for females are independent of phenotypic characteristics of their social mate. Most previous studies of extrapair paternity in socially monogamous passerines have compared extrapair males with the resident males they cuckolded, under the assumption that females would copulate with extrapair males who are of higher quality relative to their social mate (but see Johannessen et al. 2005). While there is some evidence in tree swallows that extrapair males are in better condition than males they cuckolded (Kempnaers et al. 2001), most studies have failed to detect such differences (Lifjeld et al. 1993; Dunn et al. 1994; Kempnaers et al. 1999). None the less, the high variance in male reproductive success due to extrapair paternity in this species suggests that extrapair fertilization success is not evenly distributed among males (Whittingham & Dunn 2004), as would be expected if females are consistent in their preference for extrapair males with certain characteristics, or if different males adopt different mating strategies. There is potential for this differential extrapair fertilization success to influence the strength of selection on male traits, if the ability of male tree swallows to secure extrapair fertilizations is associated with particular phenotypic characteristics. However, it remains unclear whether male extrapair mating success is associated with any morphological or behavioural characteristics in this species.

In this study, we used microsatellite profiling to identify males that sired extrapair offspring in a population of tree swallows. This allowed us to determine which phenotypic characteristics of males, if any, predict extrapair fertilization success in this species. In addition, we performed pairwise comparisons of extrapair males and the males they cuckolded to determine whether females chose extrapair mates of higher quality than their social mates. Furthermore, we investigated whether male characteristics influenced the proportion of extrapair young found in their nests.

## METHODS

### Study Area and Field Procedures

We have been studying tree swallows breeding in nestboxes near Prince George, BC, Canada (53°N, 123°W) since May 2001. The study area consists of open agricultural fields mixed with patches of coniferous and deciduous forest, and many small wetlands. The site contains 125 nestboxes mounted on fence posts, and placed approximately 20–30 m apart. In 2004, the year this study was conducted, 64 boxes were occupied by breeding pairs of tree swallows. Beginning in May, we visited nestboxes

regularly to determine clutch initiation date. Soon after the nestlings had hatched, adults feeding their young were captured in the nest using a swing-door trap. For each adult, we measured length of the right wing with a ruler (nearest 0.5 mm), and determined mass using a spring balance (nearest 0.25 g). We banded adults and 14-day-old nestlings with standard aluminium leg bands and collected blood samples from all individuals by puncturing the brachial vein. Blood samples were stored in 1 ml of Queen's lysis buffer (Seutin et al. 1991) at 4°C.

### Plumage Coloration

At the time of capture, we collected feather samples from the rump and mantle of all males. After collection, feathers were stored in small opaque envelopes at room temperature. To analyse spectral characteristics, four feathers (of the same body area and male) were taped to a black piece of cardboard in an overlapping pattern that reproduced the way feathers are naturally arranged on birds. Reflectance was assessed by the same person using an Ocean Optics USB2000 spectrometer (Dunedin, FL, U.S.A.) with a deuterium tungsten halogen light source (Avantes, Broomfield, CO, U.S.A.). We used a bifurcated probe held in a cylindrical sheath that excluded ambient light and kept the probe tip at a 90° angle, 6 mm from the feather surface. We took readings at three random locations on the feathers; spectral data were recorded between wavelengths of 300–700 nm as the proportion of light reflected relative to the reflectance of a pure white standard (Ocean Optics). To reduce electrical noise, each of the measures represented an average of 20 spectral readings taken at 100-ms intervals and smoothed with a boxcar function using a 5 data point average.

We summarized the spectral curves of each body region by quantifying measures of brightness, hue, and chroma. Average brightness ( $R_{avr}$ ), was calculated as the average percentage reflectance between 300 and 700 nm (Doucet et al. 2005). As an index of hue, we used the wavelength of maximum reflectance ( $\lambda R_{Max}$ ) recommended by Montgomerie (2006). For chroma, because the iridescent plumage of tree swallows peaks in the blue range of the spectrum, we calculated blue chroma as the relative contribution of the blue range as a percentage of the overall brightness ( $R_{400-512\text{ nm}}/R_{300-700\text{ nm}}$ ). We also calculated a measure of ultraviolet (UV) chroma ( $R_{300-400\text{ nm}}/R_{300-700\text{ nm}}$ ). Although plumage reflectance of tree swallows does not peak in the ultraviolet range of the spectrum, studies of other species have shown that UV chroma of male plumage influences female mate choice (Bennett et al. 1997; Hunt et al. 1999) and that ultraviolet reflectance may be a biologically and an ecologically important signal in birds (Hausmann et al. 2003).

Since the rump and mantle feathers did not differ within individuals for any of the four plumage descriptors that were measured (unpublished results), we used the average values of both feather types for all analyses (Doucet 2002). Data for the four plumage characteristics were then entered in a principal component analysis to eliminate the multiple correlations among the measures.

The first component, PC1, explained 53.4% of the variation and was heavily weighted by hue and UV chroma but very little by blue chroma and brightness (rotated matrix values:  $-0.92$ ,  $0.98$ ,  $0.13$ , and  $-0.15$ , respectively); PC1 therefore represented the relationship between hue and UV reflectance, with higher scores representing high UV chroma. The second component, PC2, explained 24.6% of the variation and generally represented differences in blue chroma between individuals (rotated matrix values:  $-0.31$ ,  $-0.03$ ,  $0.99$  and  $-0.01$  for hue, UV chroma, blue chroma and brightness, respectively). The third component, PC3, explained 20.4% of the variation and was heavily weighted by brightness ( $0.14$ ,  $-0.11$ ,  $-0.01$ ,  $0.99$  for hue, UV chroma, blue chroma, and brightness, respectively).

### Parentage Analysis

Details of the paternity analysis used in this study have been described in O'Brien & Dawson (2007). In short, three microsatellite regions were amplified with polymerase chain reaction using the following primer pairs: HrU6 (Primmer et al. 1995), HrU10 (Primmer et al. 1996), and IBI MP5-29 (Crossman 1996). Polymerase chain reaction products were analysed using a Beckman-Coulter CEQ 8000 automated sequencer (Fullerton, CA, U.S.A.) and offspring were matched with their biological parents using the program Cervus 2.0 (Marshall et al. 1998). The exclusion probability for all three loci (Jamieson 1994) was 0.995 with one parent known, and the probability that a randomly chosen male would share the same genotype as the extrapair offspring (Jeffreys et al. 1992) varied from  $9.4 \times 10^{-5}$  to 0.024 (mean  $\pm$  SD:  $0.0033 \pm 0.0050$ ,  $N = 32$ ).

### Data Analyses

Male tree swallows, unlike females, cannot be aged according to plumage characteristics. However, since adult male tree swallows have very high nest site fidelity (Robertson et al. 1992) and fewer than 5% of all breeding males change breeding sites throughout their lifetime (Winkler et al. 2004), males breeding on our study area for the first time are probably relatively young individuals in comparison with those males banded as adults in previous years. As a surrogate for age, we included capture status (relatively young or 'newly captured' versus relatively old or 'recaptured') in all analyses.

We used general linear models to investigate whether phenotypic characteristics of males predicted the amount of paternity lost in their own nests (dependent variable: % of young in nest sired by extrapair males). We generated 17 candidate models that included, in various biologically relevant combinations, male plumage UV chroma (PC1), plumage blue chroma (PC2), plumage brightness (PC3), capture status, mass, body size (estimated by wing length), clutch initiation date, and several first-order interactions as independent variables. The global model included all seven factors and the interactions. Since the mass of individual males decreases over the breeding period (unpublished results), we corrected for this by calculating the

residuals from a regression of mass on Julian date of capture. This measure was used instead of a body condition index (such as mass corrected for size) because previous research on tree swallows suggests that body mass can be important in extrapair mate choice (Kempnaers et al. 2001). Models were evaluated based on the comparison of Akaike's Information Criterion (AIC) values adjusted for small sample size ( $AIC_c$ ) (Burnham & Anderson 2002).

To determine which male characteristic(s) best predicted extrapair fertilization success within the population (dependent variable: 0 = did not sire extrapair young, 1 = sired extrapair young), we developed a total of 15 logistic regression models that contained, in various combinations, one or more of the following factors: capture status, plumage hue (PC1), plumage blue chroma (PC2), plumage brightness (PC3), corrected mass, body size (wing length), and clutch initiation date. The global model included all six factors. Models were evaluated based on the comparison of AIC values, adjusted for overdispersion and small sample size ( $QAIC_c$ ) (Burnham & Anderson 2002).

To determine whether females were fertilized by extrapair males that were phenotypically different than their social mates, we used paired *t* tests comparing the morphological and plumage characteristics of males that sired extrapair young with the characteristics of males they cuckolded. When two or more extrapair males were found to have sired nestlings in the same brood, we used the average value for each characteristic compared. To compare male age, we performed a McNemar change test corrected for continuity (Siegel & Castellan 1988).

Analyses were performed using SPSS® (Norušis 2000), and Intercooled STATA 9.2 (STATA 2005), and data are presented as mean  $\pm$  1 SE unless otherwise indicated. All tests were two tailed, and results were considered significant at the 0.05 level. Blood and feather samples were collected under permit from Environment Canada and our research protocols were approved by the Animal Care and Use Committee of University of Northern British Columbia.

## RESULTS

### Patterns of Paternity and Male Reproductive Success

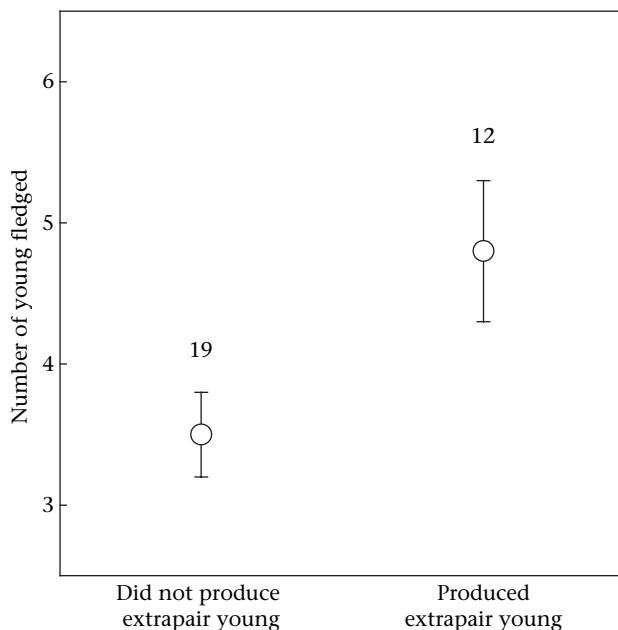
Incidence of extrapair paternity in our study population has been reported previously in O'Brien & Dawson (2007), and was similar to other estimates for this species. Briefly, of the 40 nests included in parentage analysis, 85% (34) contained offspring of mixed paternity. The average proportion of extrapair offspring in these nests was  $0.43 \pm 0.04$ ; no nests contained exclusively extrapair young. In total, 35% (76/216) of all nestlings genotyped were extrapair offspring (O'Brien & Dawson 2007). The biological fathers of 42% (32/76) of extrapair young were identified. Of the 34 nests containing offspring of mixed paternity, the biological father of at least one extrapair offspring was identified in 41% (14 nests); in nine of these nests, all extrapair young were sired by a single male. Two extrapair sires were identified in each of three broods, and three extrapair sires were identified in two broods. The biological father(s) of all nestlings in 32% (11) of broods with mixed paternity

were identified. Nineteen males were identified as the father of at least one extrapair offspring, and two of these males sired extrapair young in two nests. In all cases, identified extrapair sires were resident males who nested nearby.

Obtaining extrapair fertilizations did not influence the proportion of paternity extrapair males (EP males) lost in their own nests (proportion of extrapair offspring in nests of EP males:  $0.41 \pm 0.08$  versus  $0.32 \pm 0.05$  in nests of males who did not sire extrapair offspring (WP males); independent samples *t* test:  $t_{31} = 0.97$ ,  $P = 0.34$ ). Consequently, within-pair reproductive success of EP males ( $3.1 \pm 0.5$  young fledged) did not differ from that of WP males ( $3.5 \pm 0.3$  young;  $t_{29} = 0.73$ ,  $P = 0.47$ ). Siring extrapair offspring, however, allowed EP males to improve their total reproductive success ( $4.8 \pm 0.5$  young fledged) relative to WP males (independent samples *t* test:  $t_{29} = 2.24$ ,  $P = 0.03$ ; Fig. 1).

### Extrapair Paternity and Male Characteristics

The proportion of extrapair young in a nest was not influenced by clutch initiation date, age, corrected mass, body size (wing length), plumage UV chroma (PC1), plumage blue chroma (PC2), or plumage brightness (PC3) of the attending male. Of the 17 candidate general linear models that we tested, three had  $\Delta\text{AIC}_c$  values smaller than 2.00, the standard cutoff in model selection (Burnham & Anderson 2002). However, the best performing model, which included capture status ( $F_{1,29} = 0.74$ ,  $P = 0.40$ ), plumage UV chroma (PC1;  $F_{1,29} = 2.53$ ,  $P = 0.12$ ), and plumage blue chroma (PC2;  $F_{1,29} = 1.31$ ,  $P = 0.26$ ) as predictors, did not contain any significant independent variables and explained little of the variation in the dependant variable ( $R^2 = 0.11$ ).



**Figure 1.** Male tree swallows that obtained extrapair paternity fledged more young than males that did not obtain extrapair paternity in the same breeding population (mean  $\pm$  SE). Sample sizes indicate number of males and are shown above error bars.

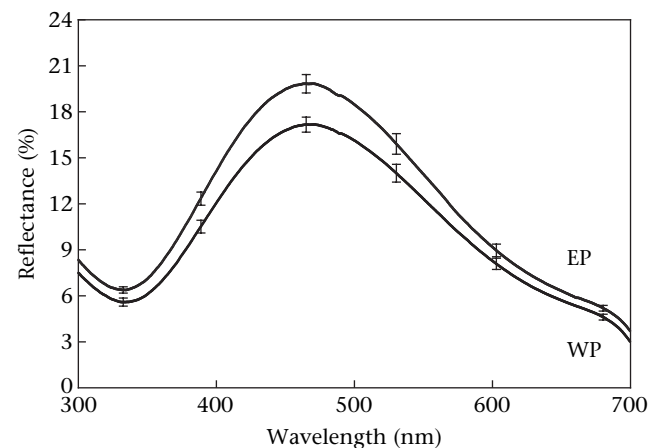
**Table 1.** Summary of logistic regression models predicting male tree swallow extrapair fertilization success

Predictors	Model likelihood	Parameters (K)	QAIC <sub>c</sub>	$\Delta\text{QAIC}_c$	Model weights
Brightness (PC3)	33.91	4	16.19	0.00	0.40
Brightness (PC3) and capture status	26.17	5	17.18	0.99	0.24
Capture status	43.02	4	18.09	1.90	0.15

QAIC<sub>c</sub>, Akaike's Information Criterion values, adjusted for overdispersion and small sample size.

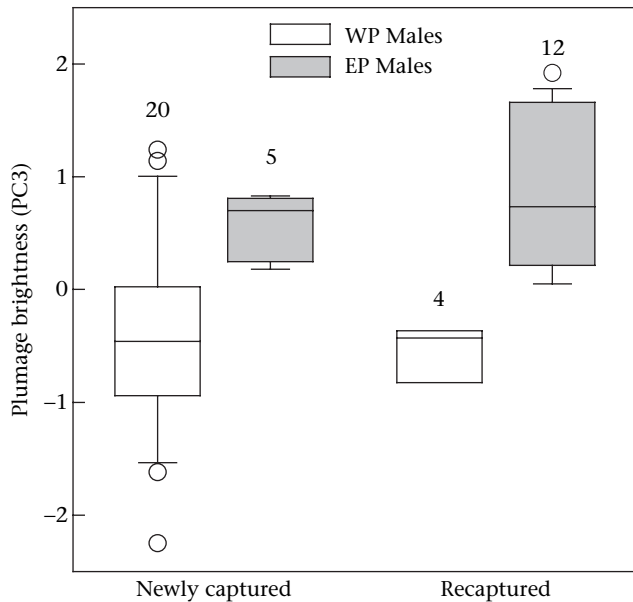
Models are presented by increasing QAIC<sub>c</sub> values. Models that have QAIC<sub>c</sub> values differing by less than 2.00 ( $\Delta\text{QAIC}_c < 2.00$ ), when compared with the lowest value, are considered equally plausible. Of 15 candidate models only those with  $\Delta\text{QAIC}_c < 2.00$  are listed.

The goodness-of-fit test for our global logistic regression model, testing which male characteristic(s) best predicted extrapair fertilization success, indicated that the model suited the data acceptably ( $P < 0.001$ ). Of the 15 candidate models that we tested, three had a  $\Delta\text{QAIC}_c$  smaller than 2.00 (Table 1). The first model included only plumage brightness (PC3) as a predictor of male extrapair fertilization success, with brighter individuals being more successful (Fig. 2). This model correctly classified 78% (32/41) of the individuals according to whether they sired extrapair young. The second model included both plumage brightness (PC3) and capture status as predictors, and correctly classified 85.5% (35/41) of males. According to this model, older (recaptured) males, as well as those with brighter plumage, were more likely to sire extrapair offspring (Fig. 3). The third model included only capture status as a predictor. Similar to the model that included only plumage brightness (PC3) as a predictor, this model also correctly classified 78% (32/41) of the individuals as WP or EP males.



**Figure 2.** Combined spectral curves of male tree swallows that did not sire extrapair young (WP;  $N = 24$ ) and males that did sire extrapair young (EP;  $N = 17$ ), averaging rump and mantle feathers. Error bars, incorporated periodically throughout the curve to show the degree of variance over the whole spectrum, represent 1 SE.





**Figure 3.** Brighter males and returning breeders were more successful at securing extrapair fertilizations than dull or newly captured males (WP = did not sire extrapair young, EP = sired extrapair young). Boxes show median (50th percentile) and interquartile range (25th–75th percentile) and whiskers indicate the 95% confidence intervals (CIs). Open circles are data points outside the 95% CI range and sample sizes are shown above each box.

When performing pairwise comparisons, we did not find any differences between extrapair males and the males they cuckolded (plumage hue PC1: mean difference  $\pm$  SE:  $-0.06 \pm 0.41$ ,  $t_{13} = 0.15$ ,  $P = 0.88$ ; plumage blue chroma PC2:  $0.04 \pm 0.31$ ,  $t_{13} = 0.12$ ,  $P = 0.91$ ; plumage brightness PC3:  $-0.49 \pm 0.34$ ,  $t_{13} = -1.43$ ,  $P = 0.18$ ; wing length  $0.05 \pm 0.73$  mm,  $t_{13} = 0.07$ ,  $P = 0.95$ ; corrected mass  $0.41 \pm 0.31$ ,  $t_{13} = 1.33$ ,  $P = 0.21$ ). In addition, the capture status of extrapair males did not differ from the males they cuckolded (McNemar change test:  $\chi^2_1 = 0.90$ ,  $P = 0.34$ ), and nests in which they sired extrapair young were not initiated earlier than their own nests ( $0.56 \pm 1.44$  days;  $t_{13} = 0.39$ ,  $P = 0.70$ ).

## DISCUSSION

Our results show that all male tree swallows are not equally successful at breeding outside the pair bond. When investigating which characteristic(s) best predicted extrapair fertilization success, the three models that fit the data equally as well strongly implied that brighter males had an advantage over dull males, and that older individuals were more likely than younger ones to secure extrapair fertilizations (Fig. 3). When both characteristics were included in the same model, 35 out of 41 individuals were correctly classified as WP or EP males (Table 1). Although plumage brightness increases with age in male tree swallows, there is considerable overlap in brightness between newly captured and recaptured birds in our population, and it is not possible to use this characteristic alone to accurately assign individuals to one of these two groups (P.-P. Bitton &

R. D. Dawson, unpublished data). It is possible that some of the bright birds that were included in the newly captured class, yet obtained extrapair fertilizations, were in fact older birds that bred elsewhere in previous years, thus increasing the apparent importance of plumage brightness in the models. This seems unlikely, however, since it has been estimated that fewer than 5% of all breeding males change breeding sites throughout their lifetime (Winkler et al. 2004). Our results therefore suggest that plumage brightness and age are independent predictors of male extrapair fertilization success, and hint at two possible complimentary aspects of the breeding behaviour of tree swallows. First, it is probable that females prefer bright males, rather than dull males, as extrapair mates. Structurally based plumage ornaments have been found to be condition dependent (e.g. Keyser & Hill 1999), reflective of nutritional stress (McGraw et al. 2002; Siefferman & Hill 2005) and parasite load (Hill et al. 2005), and thus honestly signal individual quality (Kodric-Brown & Brown 1984). By choosing individuals with bright plumage, females would be mating with high-quality individuals, potentially gaining good genes for their offspring. Indeed, females in many species are known to assess male quality, and choose a mate, based on plumage signals (reviewed in Hill 2006). Second, it is possible that older males invest more time and energy in courting females other than their social mate and/or that they are better at competing for access to receptive females. In fact, one of the most prominent correlative patterns in studies of extrapair paternity in birds is the finding that extrapair sires are older, experienced males (Griffith et al. 2002). When compared with yearlings, older individuals in some species often spend more time displaying to fertile females and intruding on other males' territories (Karubian 2002; Kleven et al. 2006), thus increasing their opportunity for extrapair copulations. In addition, it has been argued that even when patterns of refusal or acceptance of extrapair copulation by females have been linked to certain male phenotypes, the role of female choice is uncertain (Westneat 1994). For instance, females may be receptive to persistent males because the cost of resistance is too high. The benefits of consenting to such copulation attempts could equate with the benefits of seeking exclusively high-quality extrapair mates, making it difficult to differentiate between these two nonexclusive behaviours (Dickinson 2001). Unfortunately, even in well-studied species, such as tree swallows, very little is known about age-related courtship behaviour of males, limiting the inferences that can be made from this particular result. Future documentation of courtship displays of males of known age (i.e. banded as nestlings) would contribute substantially to our understanding of extrapair mating in this species. None the less, the finding that brighter males and older males are more successful at obtaining extrapair fertilizations is important, since it explains, in part, the influence of male characteristics on the realized reproductive success of individuals. In contrast, females in our population do not appear to vary their reproductive investment (clutch size or mean clutch egg mass) in relation to their social mate's morphological or plumage characteristics (all  $P > 0.10$ ; P.-P. Bitton et al., unpublished data). Therefore, the contribution of within-pair success to

a male's realized reproductive success does not seem influenced by their phenotypic attributes.

It is important to consider that there may be error in our classification of individual males as being either successful or unsuccessful at siring extrapair young. While the group composed of successful extrapair males is well defined, we could only identify the biological fathers of 42% of extrapair nestlings. It is possible, then, that males who were unsuccessful at siring extrapair offspring in our population may have in fact mated outside the pair bond with females nesting in areas other than our study site. However, if females are consistent in their mating preferences, and if male behaviour is a main factor in determining extrapair fertilization success, which seems to be the case, then our classification should be accurate. If anything, the occurrence of female mating preferences and differences in male courtship behaviour could increase the discrepancy between apparent and realized reproductive success of males, since brighter and older males would most likely produce additional undetected extrapair young outside of our study area.

Since the actual reproductive success of a male is determined by the number of young sired in his own nest and the number of young sired in other nests, individuals could improve their success by preventing the loss of paternity in their own nest, in addition to maximizing their chances of obtaining extrapair fertilizations. Observations of male tree swallows, however, have led to the conclusion that males do not spend much time guarding their social mate during the fertile period, although they might try to reduce their loss of paternity by copulating frequently (Venier & Robertson 1991; Beasley 1996). This might not be sufficient to assure paternity, as male removal experiments have failed to find differences in the proportion of extrapair young between experimental and control nests (Barber et al. 1998). Whether or not females have extrapair young in their nest might therefore be an integral component of a female reproductive strategy, irrespective of the behaviour of their social mate. Indeed, female tree swallows are known to actively fend off courting males and seem to have control over whom they mate with (Lifjeld & Robertson 1992). Which factors influence female extrapair mating behaviour is a controversial topic and has been the subject of many reviews (e.g. Ligon 1999; Griffith et al. 2002; Westneat & Stewart 2003). In our population, the proportion of extrapair offspring in a brood was not related to any phenotypic characteristics of the female's social mate. This suggests that the benefits of extrapair paternity for female tree swallows are not necessarily dependent on the quality of their social mate. It is unlikely that females in our population mated outside the pair bond to ensure against male infertility, as none of the broods in our study contained exclusively extrapair young (but see Kempenaers et al. 2001; Whittingham & Dunn 2001). Rather, this behaviour is consistent with the idea that females may seek extrapair mates to increase the genetic diversity of their offspring (Williams 1975). Such a strategy would be especially beneficial in unpredictable environments, or when the quality of potential mates is difficult to assess, and would increase the probability that at least some offspring would be successful (Westneat

et al. 1990). Supporting this hypothesis, the benefits of extrapair mating in this population have been shown to manifest themselves only under certain conditions (O'Brien & Dawson 2007).

In studies of extrapair mating strategies, female choice is usually considered to have occurred when extrapair sires are shown to be of higher quality than the social mate, based on the expression of traits that honestly reflect individual quality (Andersson 1994). This implies that females compare their social mates with potential partners and choose higher-quality individuals to gain genetic benefits for their offspring (Jennions & Petrie 2000). In studies of tree swallows, pairwise comparisons between extrapair sires and the males they cuckold have produced mixed results. While Kempenaers et al. (1999, 2001) found that extrapair males are in better condition or produce more sperm than the males they cuckolded, other studies have found little similar evidence (e.g. Dunn et al. 1994). Furthermore, it is not certain that these two characteristics are easily gauged by females and, therefore, represent reliable indicators of genetic quality. In this study, we did not detect any differences between extrapair males and the social mate they cuckolded, further supporting the idea that the benefits of extrapair paternity for female tree swallows are not necessarily dependent on the quality of their social mate. Indeed, some of the females in our population had extrapair offspring in their nests even though their social mates were very bright, and their extrapair mate(s) were therefore duller by comparison (albeit brighter than average). Instead of 'trading up', females could simply be actively pursuing extrapair mating opportunities with males of high absolute genetic quality.

While foraging, female tree swallows can travel up to 10 km from the nest site during their fertile period, and may find extrapair mates at these distant locations (Dunn & Whittingham 2005). Floater males that are difficult to capture are also known to sire extrapair offspring in this species (Barber & Robertson 1999). For these reasons, it is difficult to accurately assess the fertilization success for each male in a breeding population, and this limits our ability to estimate variance in male realized reproductive success. The best estimates produced for tree swallows so far were obtained by Kempenaers et al. (2001), who showed that 38% of the variance in reproductive success for their study population was due to the production of extrapair young. This estimate was slightly greater than the variance due to the production of within-pair young. Although we were not able to identify the sires of all extrapair offspring, our results still suggest that males that sire extrapair offspring fledge more young than males siring only within-pair offspring (Fig. 1), supporting the idea that extrapair paternity has the potential to increase the opportunity for sexual selection in this species (Webster et al. 1995; Whittingham & Dunn 2004; Kleven et al. 2006). Moreover, our finding that plumage brightness predicts male extrapair fertilization success suggests that this may be a sexually selected trait in tree swallows. Supporting this idea, males are on average brighter than females in this species (unpublished data).

Overall, our results suggest that female tree swallows do not evaluate their social mate when engaging in extrapair copulations. This is supported by the findings that (1) the proportion of extrapair paternity in females' nests was not influenced by any measured characteristics of their social mates and (2) we did not detect any differences between EP males and the males they cuckolded. Instead, our results suggest that extrapair mating behaviour in tree swallows may be a combination of age-dependent mating investment by males and female mating preference based on plumage quality. Future experimental work should be directed towards determining the relative importance of female and male behaviour in extrapair mating. Such experiments would improve our understanding of extrapair mating behaviour of tree swallows and intersexual conflicts in socially monogamous mating systems.

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