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Extra-pair paternity and the reproductive role of male floaters in the tree swallow (*Tachycineta bicolor*)

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Abstract In many avian species, a part of the population is present at the breeding grounds but does not breed. Current theories generally assume that floaters are younger or lower-quality individuals, and empirical data confirm this. However, floating could also arise as an alternative strategy to breeding, if floaters are able to reproduce via extra-pair copulations. Until the present study, there has been no evidence that floaters father offspring. We studied a population of tree swallows (*Tachycineta bicolor*), a species with one of the highest levels of extra-pair paternity known in birds. Using microsatellite markers, we determined the biological fathers of 65% of the extra-pair young. Of a total of 53 extra-pair young (52% of all offspring), 47% were fathered by local residents, 6% by residents breeding elsewhere (up to 2 km from the focal grid), and 13% by floaters. Residents seemed to be more successful and they were also more likely to return as territory holders in the next breeding season compared to floaters. Extra-pair males were on average in better condition than the within-pair males they cuckolded. Interestingly, resident males that disappeared (possibly to float) during the fertile period were heavier than males that stayed, and floaters were heavier than residents, but not different in any other characteristic. Although alternative interpretations of the data are possible, we propose that floating might be a conditional strategy in tree swallows whereby males in good condition gain more paternity via extra-pair copulations, whereas males in worse condition are more successful by providing parental care.

Keywords Sperm competition · Reproductive strategies · Paternity · Sexual selection · Variance in reproductive success

Introduction

Many studies of birds and other vertebrates have shown that a substantial part of the sexually mature population does not breed in a given year, despite being present at the breeding grounds (e.g., Smith and Arcese 1989; Mönkkönen 1990; Shutler and Weatherhead 1991). These individuals are usually referred to as “floaters” or “satellites.” There are two general explanations for why individuals end up as floaters. They could be “surplus territory contenders” (Shutler and Weatherhead 1992), i.e., individuals excluded from breeding because they were unsuccessful in the competition for a territory, nest site, or mate. Alternatively, floaters are individuals that “decide” to forego breeding in a particular year, even though breeding opportunities are available. The latter strategy could be successful if by “queuing” they are more likely to end up in a high-quality territory when the quality of the available territories is low (Zack and Stutchbury 1992; Ens et al. 1995; Kokko and Sutherland 1998).

Floaters may be able to enhance their reproductive success by alternative reproductive behavior. For example, in some species, female floaters reproduce via intra-specific brood parasitism (Gowaty 1985; Lyon 1993; Sandell and Diemer 1999). Male floaters could reproduce by performing extra-pair copulations with resident females. Because extra-pair paternity is widespread in birds (Petrie and Kempenaers 1998), floaters could potentially father many offspring without having to invest in territory defense or parental care. Intuitively, one would expect this strategy to occur frequently, but to date there is no evidence that floaters father offspring. Why would this be? First, floaters might be unsuccessful because females refuse to copulate with them. This is not unlikely if floaters are younger or lower-quality individ-

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uals and females prefer extra-pair partners that have larger secondary sexual traits, are older, or are more likely to survive (Møller and Ninni 1998). Second, floaters have rarely been included as potential fathers in studies using the appropriate molecular markers to assign paternity to extra-pair offspring.

In this paper, we report on a study of paternity in a population of the North American tree swallow (*Tachycineta bicolor*). Tree swallows show one of the highest levels of extra-pair paternity known in birds (38–69% of all young are extra-pair; review in Barber et al. 1996). However, our understanding of the origin and the consequences of this extraordinary level of promiscuity is limited. This is mainly because the biological fathers of the majority of the extra-pair young could not be identified, despite the fact that most of the resident males were sampled (Dunn et al. 1994a; Kempenaers et al. 1999). Finding the biological fathers of the extra-pair young would allow us (a) to estimate the opportunity for sexual selection by calculating the variance in true reproductive success and (b) to evaluate which male characteristics influence success in gaining paternity by comparing characteristics of social males and extra-pair males.

Tree swallows are migratory, cavity-nesting birds which show intense competition for suitable nest sites, and male and female floaters are present on the breeding grounds in large numbers every year (Stutchbury and Robertson 1985). A study of female floaters showed that they do not reproduce unless they can take over a vacant nest site (Stutchbury and Robertson 1985). Intraspecific brood parasitism is virtually absent in this species: despite many studies using molecular techniques that would have allowed its detection, only one case has been found so far (Barber et al. 1996; Kempenaers et al. 1999). Male floaters have not been studied in detail, but they could potentially have a high reproductive success through extra-pair copulations. Two recent studies provide circumstantial evidence that floaters might father offspring. Barber and Robertson (1999) monitored copulation behavior at a nestbox grid and found that two floater males achieved 5 of 17 observed extra-pair copulation attempts, at least 3 of which were successful (with cloacal contact). However, a paternity study failed to provide evidence that any of the successful extra-pair copulations (by residents or floaters) led to paternity (Barber and Robertson 1999). A study of the reproductive anatomy of male tree swallows (Peer et al. 2000) showed that floaters and residents had testes of similar size, but that floaters had a larger cloacal protuberance and thus stored more sperm than residents. Therefore, floaters could compete with residents for paternity.

The main aim of this study was to find the biological fathers of the extra-pair offspring and to assess the reproductive role of male floaters. To this end, we followed all breeding attempts on a small nestbox grid and obtained blood samples from as many potential fathers as possible. Three groups of males were sampled: (a) residents on the nestbox grid, (b) residents breeding in the surrounding area, and (c) floaters. We used a set of poly-

morphic microsatellite markers to assign paternity to extra-pair offspring. Earlier studies on similar grids have shown that extra-pair copulations are rarely observed, relative to within-pair copulations (Venier et al. 1993; Barber and Robertson 1999) and they can hardly account for the high number of extra-pair young. However, floaters might visit the nestbox grid to assess which females are fertile and follow those females, e.g. during foraging trips. Alternatively, floaters might visit the grid to take over a nestbox when a vacancy arises. Thus, we also evaluated the success of floaters in takeovers.

Methods

Study area and field procedures

The study took place near the Queen's University Biological Station (44°34' N, 76°19' W), Chaffey's Locks, Ontario, Canada, from April to July 1997. We studied tree swallows breeding on Hughson's grid which consisted of 24 nestboxes mounted on metal poles in an abandoned hayfield of approximately 160×120 m (see also Dunn et al. 1994a; Barber and Robertson 1999).

We caught adults with mistnets and with traps inside the nestbox. On the focal grid, we started capturing birds as soon as they arrived. To increase our success in capturing floaters, we scattered mistnets over the grid and we also erected extra "trapping" nestboxes at the edge of the grid, which we removed again after the banding session. We define a floater as an individual that was caught on the focal grid, but did not breed there or in any of the nestboxes in the surrounding area (see below for details). We cannot exclude the possibility that some of these individuals bred elsewhere in natural cavities, but since we rarely observed marked birds from the nearby nestbox grids on the focal grid, it seems unlikely that those individuals were breeders.

Most resident males were caught before the fertile period of their social mate. Two males, one of which had been banded in a previous year, were caught only when feeding chicks. Each bird was banded with a metal band and with a red (female) or a blue (male) color band. We also marked each individual with a unique combination of two colored spots of acrylic paint on the left wing to allow quick identification in the field. We assessed sex based on plumage characteristics and wing chord (Hussell 1983; Stutchbury and Robertson 1987), the presence of a brood patch (females) or cloacal protuberance (males), and behavioral observations. All floaters whose sex could not be determined with certainty ($n=25$) were sexed using molecular markers (see below).

For each adult, we measured the right wing length to the nearest 0.5 mm using a ruler, and the right tarsus to the nearest 0.01 mm using dial calipers. We weighed each bird to the nearest 0.1 g with a Pesola spring balance. As an index of ectoparasite load, we counted the number of holes in wing and tail feathers made by feather mites (see Dunn et al. 1994a). We took blood from the brachial vein (20–200 µl) from all individuals.

We checked each nestbox daily from the start of nest building until the start of incubation and every 3–4 days thereafter. In total we studied 21 first breeding attempts (18 of which produced at least one nestling) and three replacement broods (all producing nestlings). Three nestboxes were occupied by eastern bluebirds (*Sialia sialis*). One became available later in the season and was used for a replacement nest.

During the nestling stage (when young were 4–8 days old), we caught the feeding parents at all boxes on the focal grid. To facilitate the identification of parents during feeding observations (see below), we made a colored spot on the white breast feathers using a green (male) or red (female) marker. We also attempted to catch the males at all other active nestboxes in the area, i.e. on all the nearby grids and in solitary boxes along the road from the grids to the biological station (for details see Kempenaers et al. 1998). We

failed to catch many of those males, but we always observed them and noted their color combination if they were marked. The captured individuals were banded, measured, and a blood sample (30–150 µl) was taken for paternity analyses.

We measured the distances between solitary nestboxes and grids using a GPS-system with a precision of 5 m. The system consisted of a Trimble ProXL satellite receiver, a Trimble ProBeacon real-time differential correction signal receiver, and a Corvalis Microtechnology model MC-V datalogger unit running Asset Surveyor software.

In the 21 nests we studied, 8 of the 117 eggs that were laid did not hatch (6.8%). Five eggs showed no signs of development. Embryos from the other 3 eggs were collected and stored in ethanol. Of the 109 hatchlings, 8 disappeared and 3 were found dead in the nest before they were 6 days old. From the latter 3, brain tissue was removed and stored in ethanol. When the young were 6 days old, we took blood (15–150 µl) from the brachial or tarsal vein ($n=98$).

Behavioral observations

From the start of banding until the end of the egg-laying period, we surveyed the entire grid at least once a day and indicated the identity and location of the resident birds on a map. We also noted the presence of all marked individuals that were not occupying a nestbox.

When the young were between 6–12 days old, we counted the number of feeding trips made by the male and the female during one (ten nests) or two (seven nests) 1-h observation periods. Observations were made throughout the day, but not during periods of heavy rain. All observations were made while sitting in the field 20–30 m from the box.

Parentage analyses

Blood samples were stored in Queen's lysis buffer (Seutin et al. 1991) at 4°C. Details on the extraction of genomic DNA, PCR amplification, the origin of the microsatellite primers and other laboratory procedures can be found in Kempnaers et al. (1999). Parentage analyses were done as described in Kempnaers et al. (1999) with the following modifications. We used five microsatellite primers with a combined exclusion power of $P=0.999$ and a combined identity probability of $P=1.9 \times 10^{-8}$ (Table 1). Most nestlings (81%) were scored at all five loci, while the remainder were scored at four loci (not at HrU5). We compared the allele sizes at the scored loci with those of the putative parents. One nestling showed a mismatch at three out of five loci with the female at the nest and is thus likely the result of intraspecific brood parasitism. None of the other resident females had a genotype that matched this offspring's genotype. The genotypes of all other nestlings matched those found in the female at the nest. The genotypes of 54 out of 104 offspring were not compatible with the genotype of the social father. Three offspring (5.6%) showed a mismatch at only one locus. These offspring could be extra-pair young, or the mismatch could result from a mutation. We assumed the latter, so

that the frequency of extra-pair paternity might be slightly underestimated. Nine offspring (16.7%) showed a mismatch at two loci, 9 (16.7%) at three loci, 25 (46.3%) at four loci, and 11 (20.4%) at all five loci. These offspring were considered extra-pair young.

We assigned paternity by screening all resident and floater males for the paternally inherited alleles found in the extra-pair young. We used the conservative approach, assigning paternity only when all offspring alleles matched the genotype of the male. With our primer set, the probability that a randomly chosen male shared the same genotype as the extra-pair offspring ranged from 1.6×10^{-6} to 0.0092 (mean \pm SD: 0.0010 ± 0.0019 , $n=35$). These values might be misleading because they only reflect the true exclusion probability if the putative sires are a random selection of individuals from a panmictic study population. If related males compete for paternity, the power of exclusion will be considerably lower (Double et al. 1997). However, in tree swallows we can safely assume that putative sires are unrelated, given the low proportion of males born in the study area combined with relatively low adult survival. In our sample of putative fathers, only four males (4%) were born in the area and none of them on the focal grid. Thus, a male with a matching genotype was most likely the true biological father.

We also checked whether the alleles found in the within-pair offspring matched any of the other males' genotypes. This was the case for one young, but we assumed that the resident male was the true father (rather than one of the neighbors).

Molecular sexing

We determined the sex of 25 floaters by polymerase chain reaction (PCR) amplification of the two homologous genes *CHDIW* and *CHDIZ*. Approximately 100 ng of genomic DNA was amplified using a Perkin-Elmer 9600 thermal cycler. The total reaction volume of 10 µl consisted of 1 µl 10×Gibco BRL PCR buffer, 25 mM MgCl₂, 200 µM dNTPs, 8 ng each of the primers P2 and P8 (Griffiths et al. 1998), and 0.3 units of *Taq* polymerase. Samples were denatured at 94°C for 1.5 min and then cycled 30 times using the following parameters: 15 s at 94°C, 30 s at 52°C, and 30 s at 72°C. Samples were then held at 52°C for 1 min, followed by 72°C for 5 min, before being stored at 4°C. We used 5 units of *Hae*III in the presence of 1×ReactII buffer (Gibco BRL) to cut 5 µl of each PCR product at an incubation temperature of 37°C for at least 1 h. Samples were electrophoresed on a 2% agarose gel and visualized under UV light after staining with ethidium bromide. Twenty-one of the 25 individuals sexed as "possible male" in the field were males (one band: *CHDIZ*), the other four were females (two bands: *CHDIZ* and *CHDIW*).

Data analyses

To investigate seasonal changes in body mass and in the number of mite holes, we used data from all males captured in 1997 (at two study areas). During the pre-laying period, body mass did not change significantly with date ($P>0.5$), but depended on body size (regression with tarsus length: $r=0.25$, $n=97$, $P=0.015$). Thus, we

Table 1 Polymorphism data for the five microsatellite markers used in this study. The HrU markers were originally developed for the barn swallow *Hirundo rustica* (see Primmer et al. 1995), and IBI3–31 for the tree swallow (Crossman 1996)

Marker name	n^a	Observed heterozygosity (%)	Number of alleles	Frequency of most frequent allele	P_{identity}^b	$P_{\text{exclusion}}^{b,c}$
HrU3	120	96.7	42	0.10	0.0072	0.91
HrU5	52	94.2	30	0.14	0.015	0.87
HrU6	120	94.2	75	0.16	0.019	0.85
HrU7	120	67.5	8	0.38	0.17	0.54
IBI3–31	120	90.0	14	0.28	0.054	0.73

^a Number of unrelated adults (male and female residents and floaters)

^b Primmer et al. (1995)

^c Double et al. (1997)

report both body mass and the residuals of the regression of body mass on tarsus length as a measure of body condition. The number of mite holes increased significantly with date during the pre-laying to laying period ($r=0.36$, $n=92$, $P=0.001$). In all analyses, we used both the absolute number of mite holes and the number of mite holes corrected for date (residuals of the regression with date).

Data were analyzed using SPSS 9.0 for Windows and StatXact-3 3.1 (Cytel Software Corporation); all tests are two-tailed and data shown are the mean \pm SD unless stated otherwise.

Results

Paternity and the identity of the biological fathers

We analyzed the parentage of 104 (89%) of 117 eggs from 21 clutches (Fig. 1). One nest (5%) contained one egg (<1% of all eggs) that was apparently the result of intraspecific brood parasitism (see Methods). This nest (W4) contained four eggs that were laid on consecutive days from 12 to 15 June. Thus, there is no observational evidence that brood parasitism occurred. Neither the biological father, nor the mother, could be found among the sampled individuals.

Sixteen of the 21 nests (76%) contained at least one extra-pair young and 53 out of 104 offspring (52%) were fathered by males other than the social father. We determined the biological father of 35 (65%) of all extra-pair young: 25 young (71%) were fathered by local residents, 3 young (9%) were fathered by males that were resident elsewhere, and 7 young (20%) were fathered by floater males.

Our sample of potential fathers consisted of 19 local residents, 44 residents elsewhere, and 32 floaters. We failed to catch two local residents that disappeared at nests C1 and D6. At C1, the unmarked resident was last observed 1 day before the female laid her first egg. The next day the male at D2 was observed defending box C1 and although he copulated with the female, he did not father any offspring in C1. The D2 male did not feed the offspring in C1 (1 h observation time). Note that the disappeared C1 male could have fathered the three unassigned offspring in his own nest (in that case only one out of four young would be extra-pair). At D6, the unmarked male was last seen 3 days before the female laid the first egg. Two days later, the C5 male was observed defending the box. We observed the C5 male copulating with the D6 female and feeding the chicks at both C5 and D6 (2 h observation time). The C5 male did not father offspring at D6 or at C5 (Fig. 1). Given that we assigned paternity to all offspring at D6, it seems unlikely that the original D6 male fathered within-pair offspring (but see Discussion below).

In total, a maximum of 129 males bred in nestboxes in the surrounding area (within a radius of 6.5 km), so we sampled at least 34% of them. The ST-D1 male bred 2,050 m from the focal grid; this male was caught for the first time breeding in 1992 and was the second-oldest bird known to be present in the population in 1997. The TG-C1 male bred 565 m from the focal grid and was

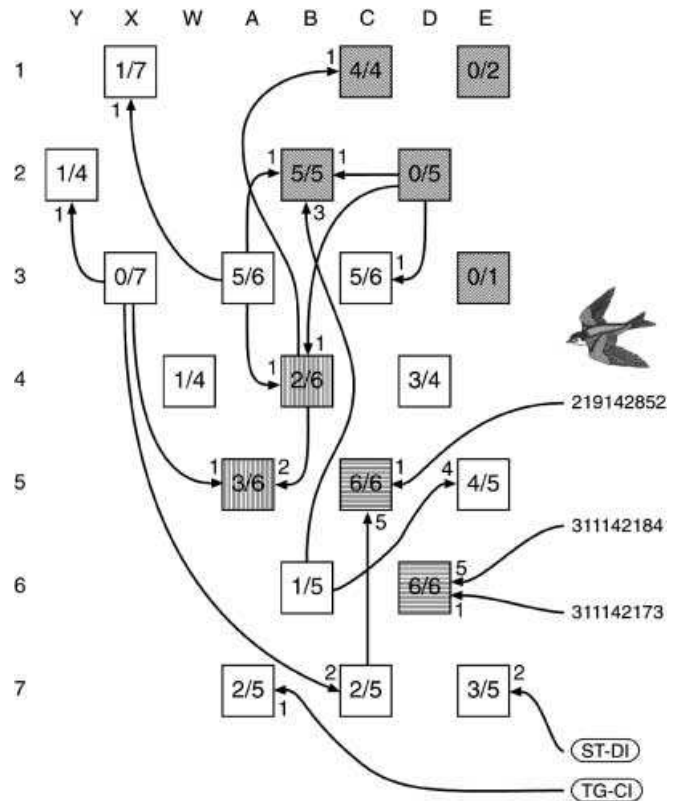


Fig. 1 Map of the nestboxes (squares) on Hughson's grid occupied by tree swallows during the 1997 breeding season. The two numbers inside each box refer to the number of extra-pair young and the total number of offspring. Arrows indicate which extra-pair males fathered offspring in a particular nest and the numbers show how many offspring they fathered. The encircled birds on the right are residents elsewhere, the birds denoted by their band number are floaters. Nestboxes marked with the same type of cross-hatching belong to one of four socially polygynous males (including takeovers)

caught for the first time. We estimate that another 50 pairs bred in natural cavities in dead trees near beaver ponds within the same area (Rendell and Robertson 1989).

The number of floaters is very difficult to estimate, but based on observations of unmarked individuals, we are unlikely to have sampled more than 25% of those that visited the focal grid. Floaters were caught between 22 April and 26 June (mean \pm SD: 8 May \pm 15 days). Laying dates (first egg) varied between 16 May and 22 June (25 May \pm 10 days). Thus, those floaters caught before 1 May and not observed afterwards had likely left the area before the fertile period of the female. This left us with 21 floaters as potential fathers. Thirteen of them (62%) were caught once and not seen again later; only 1 of those fathered offspring (311142184, see Fig. 1). The other 8 floaters were caught and/or observed on 2–9 different days and at two to seven different nestboxes; 2 of them fathered one offspring each (Fig. 1).

How certain can we be that the three males that fathered offspring and were categorized as floaters were indeed floaters? Male 311142184 was caught in a tempo-

rary box (see Methods) 1 day before the female at D6 laid her first egg and only 2 days after the unmarked resident at D6 had disappeared. Thus, we cannot exclude the possibility that the original D6 male is in fact male 311142184, who gave up his nest and became a floater. This male was never observed again. If this scenario is true, only two extra-pair young (6%) would be fathered by floaters. Male 311142173 was caught 6 days before the D6 female laid her first egg (day -6) and was observed once more on day -3. This bird was caught at box E5 and observed at B2, B4, and E5, where he was aggressively chased by the residents. Male 219142852 was caught on days -18, -12 and -8 (relative to the first egg of the female at C5) and observed on days -17, -15, -14, -11, -8, -5, and -2. We observed this male being aggressively chased by residents at A5, A7, B2, B6, C7, and E3, and he was caught once at D4 and twice at a temporary box. We cannot exclude the possibility that these males were residents elsewhere, but two observations suggest that this is very unlikely. (a) Few males marked at one grid were ever observed at another grid, despite intensive observations in two breeding seasons (our unpublished data). No marked male *known to be resident* (observed at least three times defending a box) was ever observed at another grid during the same period. (b) The identity of the males at the 129 nestboxes in the vicinity was known (marked/unmarked) and of the 32 floaters caught at our focal grid, only 1 became a resident in one of these boxes (probably several weeks after being caught at the focal grid).

Variance in male reproductive success

Figure 2 gives an overview of the within- and extra-pair reproductive success of the different categories of males on the focal grid. For the resident males ($n=19$), the mean apparent reproductive success on the nestbox grid was 4.9 ± 1.5 (range: 1–7). However, the real reproductive success was 3.9 ± 3.5 (range: 0–11). Thus, the standardized variance (i.e., the variance divided by the squared mean) in reproductive success among the residents increased from 0.09 (apparent) to 0.79 (real). The actual reproductive success of the residents will be slightly higher, given that some might have fathered young on other grids. However, we do not know how this affects

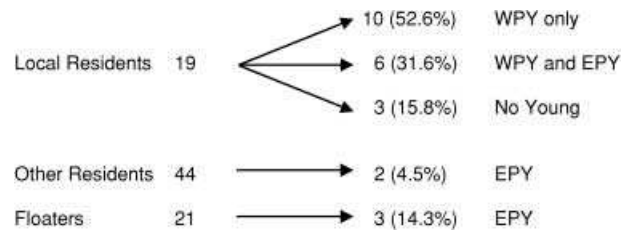


Fig. 2 Overview of the males that fathered offspring on Hughson's grid in 1997 (WPY within-pair young, EPY extra-pair young)

the variance in reproductive success. Four of the 19 resident males (21%) became socially polygynous (after takeover of one widowed female), but 6 males (32%) were genetically polygynous with an average number of 3.3 ± 0.8 partners (range: 2–4). Four out of six males that obtained extra-pair young also lost paternity in their own nest. However, the number of fathered within-pair young was significantly correlated with the number of fathered extra-pair young (Spearman rank correlation: $r_s=0.62$, $P<0.005$, $n=19$). The true reproductive success of a resident male was also highly correlated with the total number of females with whom he fathered young ($r_s=0.90$, $P<0.001$). There were no cases where males “exchanged” paternity. The timing of laying of the extra-pair males' social mate did not differ from that of his extra-pair mates (median difference in laying date=0 days, range -5 to +16).

The true reproductive success (number of young fathered) was not related to any male characteristic for the resident individuals (Spearman rank or Pearson correlations, $n=19$, all $P>0.10$). However, a pairwise comparison of the extra- and within-pair males showed that extra-pair males had on average fewer mite holes, were heavier, and were in better condition than within-pair males, but they did not differ in tarsus and wing length (Table 2).

Floaters have an apparent reproductive success of zero, but their actual reproductive success might be much higher. The average reproductive success of floaters on the local grid was $7/21=0.33$. However, the true success of floaters is hard to estimate, because it depends on the number of floaters and the number of active nests in the area covered by these floaters.

Table 2 Pairwise comparison of characteristics of within- and extra-pair males that fathered offspring in the same nest

Character	Within-pair	Extra-pair ^a	<i>n</i>	<i>t</i> / <i>T_s</i> ^b	<i>P</i>
Number of mite holes ^c	57±39	20±9	9	<i>T_s</i> =3	<0.05
Tarsus length	12.02±0.46	12.39±0.95	9	<i>t</i> =-0.95	0.37
Wing length	119.7±3.6	119.6±2.3	11	<i>t</i> =0.035	0.97
Body mass	19.9±1.4	21.9±0.7	9	<i>t</i> =-4.31	0.003
Body condition	-1.40±1.49	0.21±0.79	9	<i>t</i> =-2.78	0.024

^a If measurements of more than one extra-pair male were available, average values were used. Only measurements from individuals captured during the same period were used

^b Paired *t*-test (*t*) or Wilcoxon matched-pairs signed-rank test (*T_s*)

^c $P<0.10$ when the analysis is done with number of mite holes corrected for date of capture (see Methods)

Table 3 Information on all resident males that disappeared during the 1997 breeding season at Hughson's grid

Resident	Last observation at nest ^a	Paternity with social mate(s)	Observations after leaving nest	Takeover by
A5	-2	3/6	Becomes floater	B4 resident
B2	-4	0/5	No	D2 resident
C1	-1	max. 3/4	No	D2 resident
D6	-3	0/6	No	C5 resident
E1	+7	2/2	No	E3 resident
E5-E7	-14	0/10	No	Floater males

^a Relative to the start of laying (=day 0)

Nest desertions, takeovers, and male survival in relation to status

Our regular surveys of the nestboxes between 1 May and 9 June revealed several cases where males disappeared while their mate was still present (Table 3). These males could have died, they could have been kicked out by another male, or they could have decided to leave their nest. Interestingly, the four banded males that disappeared during the pre-laying period than the males that stayed (Fig. 3). For one of the males, we have evidence that he left his social mate to become a floater: he was observed on the grid, visiting several nestboxes, but did not return to his social mate. His female was taken over by one of the resident neighbors. We have no evidence from behavioral observations that this male left as a result of aggressive interactions with this neighbor.

All vacancies that arose during the fertile period were filled up by already paired neighbors rather than by floaters, despite the fact that floaters were present (Table 3). Thus, several resident males became socially polygynous by taking over a widowed female. On the focal grid, floaters took over two females relatively early in the season after a polygynous male (E5-E7) disappeared.

None of the 21 floaters mentioned above were caught during the next two breeding seasons, while 6 out of 19 resident males (32%) survived and bred in 1998 and 5 of them also bred in 1999. Thus, residents are significantly more likely to be territory holders during the subsequent breeding season than floaters (Fisher's exact test, $P=0.007$). However, we do not know whether this difference is due to differential survival or differential detection, because in 1998, only residents were caught.

Discussion

The reproductive role of floaters

Our data strongly suggest that floater males in our tree swallow population fathered offspring via extra-pair copulations. Previous observations that tree swallow floaters perform extra-pair copulations (Barber and Robertson 1999) and that they have well-developed reproductive organs (Peer et al. 2000) had already suggested that they could potentially father offspring, but until the present

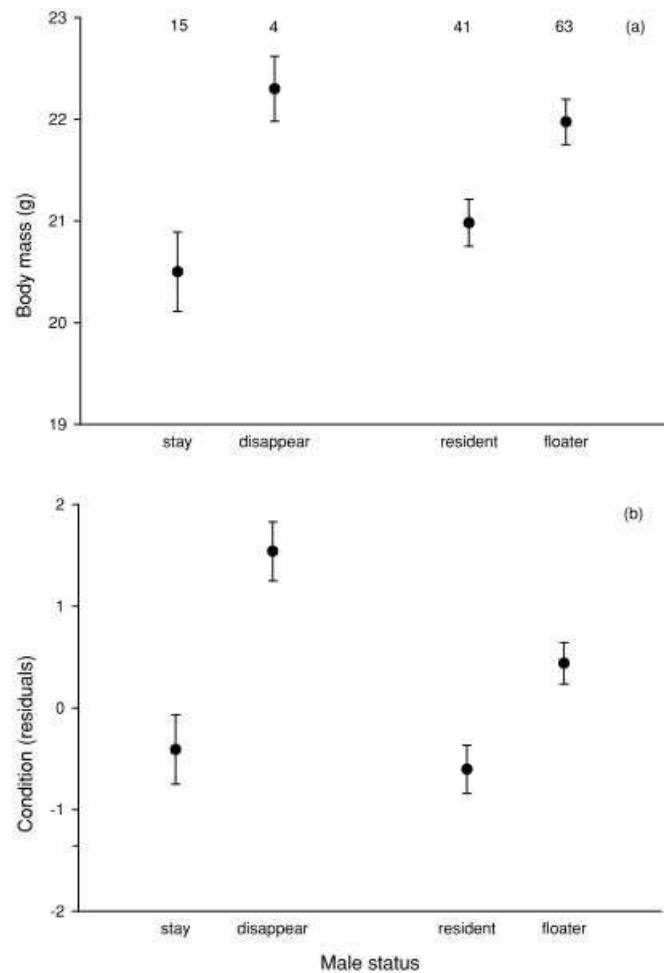


Fig. 3 Body mass (a) and condition (b) for several categories of male tree swallows. Shown are the mean and SE. On the left are shown resident males from Hughson's grid that stayed to feed their offspring versus males that deserted or died (body mass: $t=-3.38$, $P=0.0052$; condition: $t=-4.37$, $P=0.001$). On the right, the difference between resident and floater males [body mass: $t=-2.97$, $P=0.004$; condition: $t=-3.28$, $P=0.001$; combined data from the focal grid (this study) and from another study area (Peer et al. 2000)]

study, evidence was missing. To our knowledge, there is only one other study showing that floaters reproduce via extra-pair copulations (Ewen et al. 1999). However, the latter study on the stitchbird (*Notiomystis cincta*) is unusual in that it was conducted on a small island population that had recently been reintroduced and was male biased (Ewen et al. 1999).

Despite our best efforts to sample potential fathers, we only assigned the father of 65% of the extra-pair young. This is an increase of 44% compared to earlier attempts by Dunn et al. (1994a) and Kempenaers et al. (1999) for the same population. We found that two males that bred within about 2 km from the focal grid fathered extra-pair young on the grid. We cannot exclude the possibility that these males were floaters at the time they performed extra-pair copulations. On the other hand, many extra-pair copulations must take place away from the nestbox area, and since tree swallows can cover long distances in a short time, that residents breeding elsewhere also father offspring is perhaps not surprising. Tree swallows often leave the nestbox area, presumably on foraging trips, and some of our marked breeding birds were observed at a nearby lake (several kilometers away from the nestboxes). Because we only caught a fraction of the floater males and of the residents breeding elsewhere in the area, they were likely responsible for a large number of the unassigned offspring. This suggests that floaters could have fathered about a quarter to half of the extra-pair young, or up to one-quarter of all the offspring produced in 1997 on the local nestbox grid. In the previous two studies mentioned above, only 21% of the extra-pair young were fathered by local residents, compared to 47% in 1997. Thus, floaters may father an even larger proportion of the extra-pair offspring in some years.

How does the reproductive success of floaters compare to that of residents? Residents fathered an average of 3.9 offspring on the local grid. This is an underestimate of their true reproductive success, because they may have fathered some offspring on other grids. Of 44 residents caught elsewhere, 2 fathered a total of 2.9% of the offspring on the local grid. On the local grid, floaters had an average reproductive success of 0.33 offspring, but their true success is unknown. On average, residents seem to do better than floaters. Floaters would only do better if relatively few are present in the local area or if they can father offspring in many nests (in a larger area). Our estimates are restricted to one breeding season, but residents were also more likely to return to breed locally. It is hard to say something meaningful about the variance in reproductive success among floaters. Our observations suggest that there may be two categories of floater: "wandering-floaters" who are only caught or observed once at a particular area and may move over large distances and "resident-floaters" who stay for a longer period at one particular breeding site. Perhaps, it is mainly the latter category that is able to achieve high reproductive success via extra-pair copulations. Future studies might be able to use radio-telemetry to investigate home range size and reproductive strategies of floaters.

Why do individuals end up as residents or as floaters? Previous studies have shown or suggested that floaters are younger, lower-quality, or subordinate individuals (e.g., Smith 1989; Smith and Arcese 1989; Mönkkönen 1990), but this might not be true in tree swallows. Peer et al. (2000) showed that there were no differences between

residents and floaters in a number of characteristics (including the size of the reproductive organs). Most of the floaters may be yearling individuals, but there is also evidence that older birds are floating (one bird was banded in 1995 as an adult). Unfortunately, no plumage characteristic can be used to differentiate between yearling and adult tree swallow males. However, yearling females (which have a brown plumage) on average have shorter wings than adult females (yearling: 115.4 ± 2.9 , adult: 116.8 ± 2.5 , $t = -2.12$, $df = 69$, $P < 0.05$). If this is also the case in males, then our data suggest that resident and floater males do not differ in age (Peer et al. 2000). Floaters are clearly less likely to return as residents during the next breeding season compared to former residents, but we have no information on their survival.

We suggest that in our tree swallow population, males might become resident or floater as part of a flexible, condition-dependent strategy. The following evidence supports this hypothesis. (a) Some individuals change status within one season. One individual that was observed as a floater on the focal grid during the fertile period of most females later settled to become a resident (outside the focal grid), while one resident bird left his mate to become a floater. There are several other residents that disappeared close to egg-laying (Table 3). These birds could have died but, notably, they were in significantly better condition than the other local residents. (b) Birds in better condition seem to have more chances to reproduce via extra-pair copulations, because extra-pair males were on average heavier than the within-pair males they cuckolded. Extra-pair males also suffered less from ectoparasites (their feathers had fewer mite holes). Although the difference was only marginally significant, it suggests that extra-pair males were in better condition. (c) Interestingly, floaters were on average heavier than residents caught during the same period; combining data from two study areas from 1997 (Peer et al. 2000 and this study), the difference is significant (Fig. 3a). The difference remains highly significant when controlling for size (Fig. 3b). Thus, a male in good condition might do better than a male in worse condition as a floater. The former might invest more in obtaining extra-pair copulations, while the latter would do better by investing in parental care. Obviously, the benefits of either strategy would be frequency dependent and some birds invest in both parental care and obtaining extra-pair copulations.

Our morphological data on residents and floaters can, however, be interpreted differently. The lower body mass and condition of residents compared to floaters might reflect the difference in energy demands of each role. Defending a nestbox and a partner might be more costly than being a floater. This does not explain why residents that are heavier or in better condition are more likely to leave their mate. However, one could argue that body mass or condition (i.e., body mass corrected for size) is negatively correlated with individual quality. This may seem counter-intuitive, but studies on strategic regulation of body mass have shown that subdominant individuals store more fat

than dominant ones (Ekman and Lilliendahl 1993; Gosler 1996; Cuthill et al. 1997). This result has been interpreted as a response by the subdominants to a less predictable food supply, because they are more often displaced from feeding sites. Tree swallows do not defend feeding territories or sites, but the availability of their food (insects caught in flight) is strongly weather dependent (e.g., foraging success is reduced during periods of rain). Thus, one could argue that low-quality individuals are more susceptible to bad weather and therefore store more fat. This would then suggest that floaters and resident males that disappeared were in fact lower-quality individuals. It then becomes difficult to understand why extra-pair males were heavier than the within-pair males they cuckolded. Clearly, our hypothesis that floating is part of a flexible condition-dependent strategy needs further investigation.

One puzzling observation of this study is that birds that disappeared just before egg-laying (Table 3) were not replaced by floaters, as one would expect if floaters are waiting to take over an available nest site. When Lifjeld and Robertson (1992) experimentally removed resident males on the day the first egg was laid, they found that in five out of ten cases, the nearest resident neighbour took over the female, while in the other five cases, a floater male took over the widow. In 1999, we conducted a similar study and found that about half of the removed males were either not replaced or replaced by a neighbour, despite evidence that floaters were still present (our unpublished data). These observations again suggest that floaters are not simply waiting for a vacancy to arise.

Extra-pair paternity and sexual selection

Tree swallows show unusually high levels of extra-pair paternity. This study confirms previous reports (reviewed in Barber et al. 1996) that the majority of the nests contain at least one extra-pair young, that about half of all the offspring produced in a given season are extra-pair and that several resident males do not father a single offspring with their social mate. So far, our understanding of this extraordinary system was limited because of the difficulties determining the biological fathers of most of the extra-pair young (Dunn et al. 1994a; Kempenaers et al. 1999). This study was more successful and allows us to address several important issues.

The pursuit of extra-pair copulations might be costly for males in that it might lead to lower within-pair success. For example, males might have to trade off investment in mate or nest guarding with investment in the pursuit of other females. Furthermore, copulating with several females could lead to sperm depletion, particularly in tree swallows where within-pair copulations are very frequent. Males might thus also face a trade-off between sperm allocation to their own or to extra-pair females. However, this study shows that the within- and extra-pair success of males is positively correlated. This might be related to breeding synchrony if successful

males are those that breed relatively early or late compared to the majority of birds. In that case, a male could, e.g., first guard his own mate and exclusively copulate with her until her clutch is finished, and then switch to investing in extra-pair copulations. However, we found that the females of successful extra-pair males did not differ in the timing of laying compared to other females. This suggests that the breeding synchrony in this population has little effect on extra-pair paternity, as found in other species (e.g., Kempenaers 1997; Yezerinac and Weatherhead 1997; but see Saino et al. 1999).

Historically, the importance of sperm competition for sexual selection was more or less ignored (Andersson 1994), but it has recently received some well-deserved attention (Møller 1998). Because extra-pair paternity is so frequent in tree swallows, sperm competition has a potentially strong impact on sexual selection in this species. The opportunity for sexual selection depends on the variance in male reproductive success. For the resident males in our 1-year study, the ratio of the variances of realized over apparent reproductive success V_R/V_A equals 8.89, which is the second highest value compared to those reported in Møller (1998, Table 2.3). Thus, the occurrence of sperm competition seems to increase the potential for sexual selection in tree swallows. Ideally, however, floaters should be included in these calculations (which would need a paternity study on a much larger scale) and one should measure lifetime fledgling production. Sexual selection does not occur if males are inconsistent in their success in sperm competition. Although sufficiently detailed data on male success are still lacking, Dunn et al. (1994b) found no repeatability of the percentage of offspring fathered by resident males in different broods. Furthermore, it is still unclear which characteristics (behavioral, anatomical, physiological) are related to male breeding success, although body condition and sperm production seem to play a role (Kempenaers et al. 1999; this study).

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