

REPRODUCTIVE ANATOMY AND INDICES OF QUALITY IN MALE TREE SWALLOWS: THE POTENTIAL REPRODUCTIVE ROLE OF FLOATERS

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ABSTRACT.—Avian populations often consist of breeding residents and nonbreeding floaters. It is usually assumed that floaters are lower-quality individuals that do not reproduce, but floater tactics and potential reproductive success have rarely been examined carefully. To assess the potential reproductive role of male floaters in Tree Swallows (*Tachycineta bicolor*), we compared their reproductive organs and morphology with those of resident males. Tree Swallows show high levels of extrapair paternity, but two studies attempting to find the fathers of the extrapair offspring have been remarkably unsuccessful. Floater males that father extrapair young would face intense sperm competition. Theory predicts that under intense sperm competition, selection favors males that produce more sperm. Comparative studies in birds and other taxa provide evidence that the level of sperm competition influences relative testes size and sperm production. However, intraspecific adaptations to different levels of sperm competition have received far less attention. Floater Tree Swallows did not differ from resident males in any of the characters we measured, including testes size, but floaters had significantly larger cloacal protuberances. Thus, our results do not confirm the general assumption that floaters are lower-quality individuals that do not reproduce. Furthermore, floaters showed high variation in the volume of the cloacal protuberance (reflecting sperm numbers), which suggests that they engage in copulations. We conclude that floater male Tree Swallows invest heavily in sperm production (as do resident males) to exploit breeding opportunities through takeovers or extrapair copulations. Received 17 November 1998, accepted 5 May 1999.

IN SPECIES with internal fertilization, sperm competition occurs when the sperm of two or more males are present in the female reproductive tract and compete for fertilization of the eggs (Parker 1970). Most bird species are socially monogamous, but extrapair copulations (EPCs) leading to extrapair paternity are widespread (Westneat and Webster 1994, Gowaty 1996, Petrie and Kempnaers 1998). Thus, a pair male's sperm often has to compete with sperm of other males. Theoretical and empirical studies have predicted or shown that factors such as sperm numbers, sperm quality, and the timing of insemination relative to oviposition influence a male's fertilization success (e.g. Parker 1984, Birkhead et al. 1995b, Colegrave et al. 1995, Birkhead and Biggins 1998). All experimental studies to date have been done on

domestic birds, and the relative importance of these factors in wild birds is still unknown. Comparative studies show that species with high levels of sperm competition have relatively larger testes, bigger cloacal protuberances, and longer sperm (Briskie and Montgomerie 1992, Birkhead et al. 1993, Møller and Briskie 1995, Briskie et al. 1997). The first two can be seen as adaptations to produce larger ejaculates, as would be expected if sperm competition is a strong selective force.

Most studies have focused on interspecific differences in male adaptations to sperm competition. However, individuals of one species may face different levels of sperm competition, leading to differential investment in sperm production (Stockley and Purvis 1993, Stockley et al. 1994, Gage et al. 1995). In birds, such different reproductive tactics are not documented, but a population often consists of breeding residents and a substantial number of nonbreeding floaters. In contrast to breeding individuals, the behavioral tactics and potential repro-

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ductive success of floaters have received little attention. Past studies have shown or suggested that floaters are younger, lower-quality, or subordinate individuals that are excluded from breeding by dominant residents (Smith and Arcese 1989, Mönkkönen 1990, Lozano 1994). Thus, it is often assumed that floaters do not reproduce at all. Alternatively, floaters may reproduce by engaging in extrapair copulations. Floaters often are difficult to observe, but one way to elucidate their reproductive role is to study their reproductive anatomy. If floaters are indeed subordinate or lower-quality individuals, we expect their testes to be relatively small or undeveloped. They would have little or no chance to fertilize eggs because females are unlikely to perform extrapair copulations with such males (Smith 1988, Houtman 1992, Kempnaers et al. 1992, Møller 1992).

By not investing in gamete production, floaters can save energy for the next breeding season. On the other hand, if floaters pursue an alternative tactic (i.e. reproduce exclusively by performing EPCs), their reproductive organs should be bigger than those of the residents. Floaters would be exposed to higher levels of sperm competition because their sperm always have to compete with those of resident males, whereas not all residents are paired to females that engage in EPCs (Møller and Briskie 1995). Furthermore, within-pair copulations are probably more frequent than EPCs, and pair males would thus have an advantage in terms of number of sperm transferred. Because floaters do not have to engage in energetically costly territorial defense, they could invest more in sperm production to make up for this difference by means of larger ejaculates.

Tree Swallows (*Tachycineta bicolor*) are secondary cavity nesters, and breeding opportunities are limited by the availability of suitable nest sites (Leffelaar and Robertson 1984, Beasley 1996). This situation creates a large population of nonbreeding male and female floaters (Stutchbury and Robertson 1987). Tree Swallows have one of the highest levels of extrapair paternity among socially monogamous birds (Barber et al. 1996). Dunn et al. (1994) and Kempnaers et al. (1999) attempted to identify extrapair fathers in Tree Swallows using DNA fingerprinting. Despite sampling all locally resident males, the biological fathers of only 21% of the extrapair young were found. Thus,

floaters or resident males outside the study area must have fathered extrapair young. During the females' fertile period, within-pair copulations are very frequent in Tree Swallows (Venier and Robertson 1991). Thus, sperm transferred during an EPC will have to compete with a large number of rival sperm.

The aim of this study is to evaluate the potential reproductive role of male floaters in Tree Swallows and to assess whether floater males exhibit adaptations to high levels of sperm competition. We compare the reproductive anatomy and some other characteristics that may indicate quality or condition of floater and resident males.

STUDY AREA AND METHODS

Field work was carried out during April to June 1997 near the Queen's University Biological Station (44°34'N, 76°19'W), Chaffey's Locks, Ontario, Canada. We set up a grid of 31 nest boxes in an open field; boxes were put 30 m apart along rows. We caught the settling birds with mist nets or inside nest boxes, banded them with numbered leg bands, and individually marked them using acrylic paint on the wing and/or tail feathers. We determined sex based on plumage characteristics and wing chord (Hussell 1983, Stutchbury and Robertson 1987), by the presence of a cloacal protuberance, and via behavioral observations. For each individual we measured wing and tarsus length using calipers and we estimated muscle score (index from 0 to 3 depending on the amount of muscle tissue covering the sternum) and fat score (index from 0 to 8 depending on the amount of visible subcutaneous fat). We weighed each bird using a Pesola balance and counted the holes in wing and tail feathers caused by feather mites (Acariformes) as a measure of parasite load (see Dunn et al. 1994). For males, we measured the height (h) and diameter (d) of the cloacal protuberance (CP) using calipers. We calculated CP volume as:

$$\pi d^2 h / 4, \quad (1)$$

assuming a cylindrical shape. In total we banded and measured 63 males (including all the resident males on the grid), 102 females, and 29 birds of unknown sex.

In addition to daily observations, we systematically surveyed the entire grid every second day to determine which birds were residents. An individual was considered a resident when it was observed entering the box or sitting on the box with a partner on at least three consecutive surveys. We classified individuals in the grid as floaters if they were either unmarked, or marked but not behaving as a resident. Resident males spent most of their time in or on their

TABLE 1. Measurements of testis size and mass, seminal glomerus mass, and sperm numbers in male Tree Swallows of different social status (residents vs. floaters). Values are $\bar{x} \pm SE$, with n in parentheses.

	Residents	Floaters
Testis and glomerus size		
Right testis length (mm)	9.58 \pm 0.18 (12)	9.47 \pm 0.24 (11)
Left testis length (mm)	10.43 \pm 0.23 (11)	10.09 \pm 0.22 (10)
Right testis width (mm)	7.22 \pm 0.13 (11)	7.07 \pm 0.09 (11)
Left testis width (mm)	6.55 \pm 0.17 (11)	6.66 \pm 0.13 (10)
Right testis height (mm)	8.16 \pm 0.22 (10)	8.12 \pm 0.12 (11)
Left testis height (mm)	8.17 \pm 0.23 (11)	8.00 \pm 0.17 (10)
Combined testes mass (g)	0.659 \pm 0.032 (10)	0.631 \pm 0.029 (10)
Seminal glomerus mass (g) ^a	0.068 \pm 0.004 (12)	0.069 \pm 0.006 (11)
Number of sperm ($\times 10^6$)^a		
Precopulation period	35.18 \pm 5.96 (4)	24.40 \pm 7.58 (5)
Copulation period	17.70 \pm 3.06 (8)	30.83 \pm 7.78 (6)
Periods combined	23.52 \pm 3.66 (12)	27.91 \pm 5.29 (11)

^a From left seminal glomerus.

nest box, whereas floaters typically were seen briefly visiting several nest boxes before disappearing from the field. Floaters never stayed at one box for a prolonged time and often were chased by residents. Some marked individuals returned to our grid repeatedly, visiting several nest boxes but never settling; these individuals were categorized as floaters.

In this and a related study, marked residents rarely were observed at neighboring grids (six grids between <1 and 10 km apart), and when seen on other grids they did not behave as floaters (i.e. visiting nest boxes; unpubl. data). Thus, we consider it very unlikely that the birds we categorized as floaters were residents elsewhere. Of the 63 males captured, 30 were categorized as floaters and 27 as residents. The status of six individuals was unclear, and they were excluded from analyses. We checked nests every second day and recorded the start of nest building and the first-egg date for each pair. All nest boxes on the grid were occupied by either Tree Swallows or Eastern Bluebirds (*Sialia sialis*).

During the presumed fertile period of females (see Birkhead and Møller 1992), i.e. between the start of nest building and a few days before the end of egg laying (7 to 23 May), we killed resident ($n = 13$) and floater ($n = 11$) males and dissected them in the field. We also collected four males during the first days of settlement (15 to 16 April) to determine whether their testes were already developed. Birds were either shot or captured with mist nets and killed by thoracic compression; all birds were collected under license. We removed the reproductive organs (testes, vas deferens and the cloacal area including the seminal glomera) and stored them in 10% buffered formalin.

We examined the reproductive organs in the laboratory following the general methods described in Birkhead et al. (1991). In brief, we measured length, width, and height of the left and right testis. We

weighed both testes and the left seminal glomerus to the nearest 0.0001 g on an electronic balance. We estimated the total number of sperm in the left seminal glomerus using an Improved Neubauer and a Bürker-Türk counting chamber. Because the numbers of sperm in the left and right glomera are highly correlated (T. R. Birkhead pers. comm.), we did not count the sperm in the right seminal glomerus.

Sample sizes do not always correspond to the number of birds collected, because in some samples one or both testes or seminal glomera had been damaged during collection. Data were analyzed using Statistica 5.1 following Sokal and Rohlf (1995); all tests are two-tailed, and unless indicated otherwise, data shown are $\bar{x} \pm SE$.

The numbers of sperm in the seminal glomera depend on the frequency of copulations; i.e. birds that have recently copulated will have lower sperm numbers because of sperm depletion (Birkhead 1991, Birkhead et al. 1994; but see Westneat et al. 1998). Therefore, we compared sperm numbers for individuals collected before frequent copulations were observed (precopulation period) with those of individuals that had started to copulate (copulation period). We classified resident males into one of these periods based on direct observations, their female's first-egg date, or the state of development of their female's ovaries (some females were dissected for another study). We assumed that frequent copulations started four days before the first egg was laid (based on observations on the grid). We classified floaters based on the mean first-egg date for the population, again assuming that copulations started four days before laying.

All testis measurements (Table 1) were highly correlated with testis mass (for both left and right testis; all $P < 0.001$), and seminal glomerus mass (Table 1) was correlated with sperm numbers ($r = 0.81$, $n =$

23, $P < 0.001$). Thus, for further analyses, we used only combined testes mass and sperm numbers.

RESULTS

The reproductive organs of the individuals collected upon arrival were hardly developed: we could not detect any seminal glomera, and the combined testes mass was only about 10% of that of the breeding residents (arrivals, 0.0520 ± 0.0075 g, $n = 4$; breeders, 0.6588 ± 0.0032 g, $n = 10$; t -test with separate variance estimates, $t = -18.66$, $df = 9.94$, $P < 0.0001$). These early arriving birds are excluded in further analyses.

Floaters and residents did not differ in combined testes mass ($t = 0.65$, $P = 0.53$) nor in the number of sperm in the left seminal glomerus ($t = -0.69$, $P = 0.50$; Table 1). However, the number of sperm in the seminal glomera depended on the period (precopulation vs. copulation) and on the status of the individuals. Floaters tended to have more sperm in their seminal glomera than residents during the copulation period, but not during the precopulation period (Table 1). Despite small sample sizes, this effect approached significance (two-way ANOVA with status and period as factors, interaction term, $F = 3.74$, $df = 1$ and 19 , $P = 0.068$).

Because the cloacal protuberance is formed by the seminal glomera, we can expect CP size to be correlated with the size of the seminal glomera and/or with sperm numbers. This was indeed the case (seminal glomerus mass, $r = 0.43$, $n = 23$, $P < 0.05$; sperm number, $r = 0.42$, $n = 23$, $P < 0.05$). Thus, we can use our data on CP volume, based on measurements from all males captured during the nest-building and egg-laying periods, to further investigate the difference between residents and floaters. During this period, CP volume increased significantly and linearly with date ($r = 0.56$, $n = 38$, $P < 0.001$; each individual used only once). Consequently, to control for the effect of date, we used the residuals from the regression of CP volume with date. Floaters had significantly larger CPs than did residents (t -test with separate variance estimates, $t = 2.31$, $df = 33.49$, $P < 0.05$; Fig. 1). Also, the variance in CP volume was significantly higher in floaters than in residents ($F = 4.46$, $df = 22$ and 13 , $P < 0.01$). Because larger means can be associated with

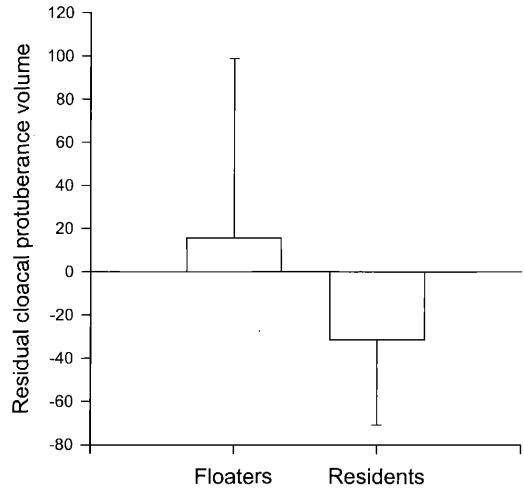


FIG. 1. Residuals ($\bar{x} \pm SD$) of the regression of cloacal protuberance volume with date for floater ($n = 23$) and resident ($n = 14$) male Tree Swallows.

higher variances as a statistical artifact, we also calculated coefficients of variation for the two groups. The coefficient of variation for CP volume for floaters (52.6%) was almost twice as high as that for residents (26.9%). We note that the variance in combined testes mass did not differ between the two groups ($F = 1.16$, $P > 0.8$; cf. Table 1).

Finally, we compared some other characters of residents and floaters that might indicate male quality or condition. Floaters and residents did not differ in average wing length, tarsus length, body mass, number of mite holes, or muscle and fat scores (Table 2). Also, we found no differences in the variance of any of these characters between floaters and residents (F -test, all $P_s > 0.3$).

DISCUSSION

In many bird populations, substantial numbers of individuals are floaters, but their role in reproduction has rarely been studied (Zack and Stutchbury 1992). Our results clearly show that the reproductive organs of floater male Tree Swallows were equally developed as those of resident males. Several conclusions can be drawn from this finding. First, we can exclude the possibility that Tree Swallow floaters are nonreproductive young birds, because if they were, their reproductive organs should have been poorly developed or not developed at all.

TABLE 2. Characteristics of male Tree Swallows of different social status (residents vs. floaters). Values are $\bar{x} \pm SE$, with n in parentheses.

Variable	Residents	Floaters	P^a
Wing length (mm)	120.70 \pm 0.51 (27)	120.18 \pm 0.51 (30)	0.47
Tarsus length (mm)	12.41 \pm 0.07 (27)	12.45 \pm 0.08 (30)	0.65
Body mass (g) ^b	21.1 \pm 0.3 (26)	22.0 \pm 0.4 (29)	0.08
Mite holes ^c	-0.71 \pm 7.16 (20)	3.51 \pm 7.02 (27)	0.68
Muscle score	2.0 \pm 0.1 (26)	2.2 \pm 0.1 (26)	0.12
Fat score	2.8 \pm 0.2 (26)	2.9 \pm 0.1 (26)	0.67

^a P -values based on t -tests for all variables except muscle score and fat score, which are based on Mann-Whitney U -tests.

^b Only data from birds weighed during nest building and egg laying included.

^c Data are residuals of the regression of number of mite holes with date ($r = 0.34$, $n = 50$, $P < 0.025$).

Studies of Black-headed Grosbeaks (*Pheucticus melanocephalus*) and Red-winged Blackbirds (*Agelaius phoeniceus*) have shown that immature males have smaller testes than breeding males (Wright and Wright 1944, Hill 1994).

Second, floaters are not necessarily lower-quality individuals with no chances to obtain EPCs, because (1) floaters had fully developed reproductive organs, and (2) we found no differences between floater and resident males in several characters that may indicate quality or condition (Table 2). Aviary and field studies of several species have shown that testosterone levels (which are largely responsible for the control and maintenance of spermatogenesis; Farner and Wingfield 1980, Reyer et al. 1986) and the maturation of male reproductive organs are influenced by the presence of females and/or pairing status (Haase et al. 1976, Delville et al. 1984, Dufty and Wingfield 1986, Sax 1996). These studies indicate that the development of the reproductive organs is not dictated solely by seasonal effects, but also depends on social cues. Thus, males of many species invest in the development of their reproductive organs only if they have access to females, i.e. if they can potentially father offspring. Floaters could still be of lower quality than residents, because many potentially important characters on which female choice could be based, such as age, plumage color, or behavior, were not measured in this study. However, the fact that Tree Swallow floaters develop equally big testes as residents suggests that they often have the opportunity to copulate.

Third, our data did not support the idea that floaters pursue a different reproductive tactic than residents. Even though different mating tactics within populations have been documented in a variety of taxa (Moore 1991, An-

dersson 1994), the only clear example of adaptive variation in gonad size relative to reproductive tactics is found in fish (Taborsky 1998). In many fish species, large territorial males build nests and attract females, whereas small sneaker males wait until a territorial pair is spawning and then ejaculate over the female's eggs. Because sneaker males will always be in a situation of intense sperm competition with residents, they invest relatively more in sperm production, i.e. they have a higher gonadosomatic index (Gage et al. 1995). If floater Tree Swallows have similar adaptations, their testes should be bigger than those of the residents. Given the high rate of extrapair paternity in Tree Swallows, individuals specializing in performing EPCs potentially could obtain high reproductive success. Perhaps increased energy expenditure associated with large gonads puts an upper limit on testis size in a species that relies almost exclusively on flying to obtain food.

Physiologically, floater Tree Swallows clearly are capable of fertilizing eggs. There are two explanations (not mutually exclusive) for why floaters have fully developed reproductive organs. First, it allows floaters to exploit any breeding opportunity that might arise through vacancies or takeovers. Lifjeld and Robertson (1992) created experimental vacancies on the day the female laid her first egg and showed that some of the replacement males fertilized eggs. Natural replacements occur frequently in our population (30% of 23 breeding males on a grid; unpubl. data from 1995). Second, floaters can father offspring through EPCs. No evidence supports this, but floaters have not been the focus of a paternity study. Our data on cloacal protuberance size might give some indication of the male's copulation behavior. Sperm

reserves can decrease rapidly as a consequence of repeated copulations (Birkhead et al. 1995a; but see Westneat et al. 1998). If CP size is determined by the size of the seminal glomera, it might reflect past copulation behavior because a strong correlation exists between seminal glomera mass and sperm numbers (see above). During the female's fertile period, when residents copulate frequently, floaters have bigger cloacal protuberances. However, the high variation in CP size of floaters may indicate that floaters sometimes copulate, as reported by Barber and Robertson (1999). It is unlikely that the high variation in CP size is a consequence of the floater population being more variable in general, because variance in testis size and other morphological characters did not differ between residents and floaters. It is difficult to assess mating frequencies of floaters, because EPCs are rarely observed (Barber and Robertson 1999), but considering their generally large CP volumes, it is unlikely that floaters copulate very often. The "passive sperm-loss" model shows that even a single extrapair copulation can result in high levels of paternity, provided a large amount of sperm is transferred at the right time (Birkhead et al. 1988, Colegrave et al. 1995). Thus, despite infrequent copulations, floaters might have a relatively high chance to fertilize eggs if they can produce relatively large ejaculates.

The average combined testes mass of Tree Swallows (0.65 g) is almost twice what one would expect for a bird of this size (0.33 g for an average body mass of 21.6 g; Møller 1991). Having large testes is probably an adaptation to high levels of sperm competition. Studies that have attempted to find the genetic fathers of extrapair offspring found that in most cases, the fathers were nearby resident neighbors (e.g. Gibbs et al. 1990, Wetton et al. 1995, Yezerinac et al. 1995, Hasselquist et al. 1996, Kempnaers et al. 1997). However, in Tree Swallows, this does not seem to be the case (Dunn et al. 1994, Kempnaers et al. 1999). If floaters indeed compete with residents over paternity, then this could explain the large number of unidentified extrapair fathers (Dunn et al. 1994, Kempnaers et al. 1999). An alternative explanation is that migrating females copulate en route before pair formation on the breeding grounds (Quay 1985, Briskie 1996). But because none of the arriving male Tree Swallows we collected ($n = 4$)

had developed testes or any detectable seminal glomera, and because arriving females do not have developed sperm-storage tubules (unpubl. data), the extrapair fathers must be among the birds on the breeding grounds.

In conclusion, our study suggests that Tree Swallow floaters are reproductively active and have the potential to outcompete resident males in sperm competition. Whether floaters are fathering extrapair offspring should be investigated via paternity analysis. We hope that our study will encourage investigations into the reproductive role of floaters in other species. Male floaters might have fully developed reproductive organs in species for which breeding is limited by the availability of nest sites, but where opportunities to reproduce via takeovers or EPCs are frequent.

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