

Search costs influence the spatial distribution, but not the level, of extra-pair mating in tree swallows

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Abstract Costs of searching for a mate are an important component of models of sexual selection, yet they have rarely been examined in wild populations of vertebrates. In this paper, we report an experiment in which we handicapped female tree swallows by clipping some flight feathers. This manipulation increased the costs of flight and searching for extra-pair mates. Despite these costs, handicapped females had the same level of extra-pair mating (percentage of extra-pair young, percentage of broods with extra-pair young, and the number of extra-pair sires per brood) as control females. However, handicapped females were more likely to have young sired by extra-pair males that lived closer to her nest than control females. This change in the distribution of extra-pair mating was most likely due to female choice rather than male coercion, and it suggests that extra-pair mating has significant benefits to females. One important implication of our study is that ecological and social factors that influence search costs could affect the spatial distribution of extra-pair sires and, consequently, the intensity of sexual selection. These effects may have been overlooked in previous studies that did not identify extra-pair sires.

Keywords Mate choice · *Tachycineta bicolor* · Extra-pair paternity · Sexual selection · Handicapping

Introduction

Females may expend considerable time and energy searching for and mating with males (Milinski and Bakker 1992), and they may also incur an increased risk of predation (Gibson and Langen 1996). These costs of mating are key components of models of mating preferences and sexual selection (Houle and Kondrashov 2002; Kokko et al. 2002), but they have been difficult to measure empirically (Kotiaho 2001).

Theory predicts that individuals should become less choosy as costs increase (Real 1990; Crowley et al. 1991), and several studies have measured or manipulated costs to test this prediction (reviewed in Jennions and Petrie 1997). For example, fish were less likely to choose a preferred mate if forced to swim against a current (Milinski and Bakker 1992; Wong and Jennions 2003), and crickets were less likely to move toward a preferred call type when the risk of predation was greater (Hedrick and Dill 1993). These changes in choosiness are often influenced by the condition of individual females, and they have implications for the strength of sexual selection on male traits.

We might expect females in poorer condition to allocate more of their time and energy to self-maintenance and less to assessing mates. As a consequence, individual differences in condition and mate choice could affect sexual selection in two ways (Syriatowicz and Brooks 2004). First, females in poorer condition may perform less sampling and mate with males possessing a wider range of traits than females in better condition, who have relatively more time and energy to find males with superior traits. Populations with more variation in female condition would have a wider range of successfully mating males and weaker sexual selection on male traits. Alternatively, if females in poorer condition are less responsive to male mating displays, then only the most attractive males

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may be able to overcome the low responsiveness of females and attract a mate. These populations would have a smaller range of successfully mating males and stronger sexual selection. Examples of both of these outcomes have been reported in insect populations (reviewed by Syriatowicz and Brooks 2004; Hunt et al. 2005). In general, much less is known about mate sampling and its costs in vertebrates, particularly in wild populations.

Testing the effect of sampling costs and female condition on mate choice can be difficult because in many cases it is not clear whether females are choosing mates for their heritable genetic benefits or their material resources (food and parental assistance), which may not be heritable. In terms of understanding sexual selection, it is important to differentiate between these two types of benefits to females. To avoid this problem, many studies have examined mate choice in species in which females only choose mates based on the quality of male genes that will be inherited by offspring (indirect benefits). For example, in lekking species and species with extra-pair mating, females are generally thought to choose mates based on their potential to improve the genotypes of offspring, as these males provide no resources or parental assistance to females.

Most studies of extra-pair mating have focused on the potential benefits to females and very little is known about the potential costs, the largest of which are likely to be the time and energy spent assessing males. Recent theoretical and empirical studies suggest that the indirect benefits of mate choice are likely to be small (Kirkpatrick and Barton 1997; Arnqvist and Kirkpatrick 2005). In this case, we would expect extra-pair mating to be maintained only when the costs of assessing males and gaining an extra-pair mating are relatively low. Thus, it is important to understand the costs and benefits of extra-pair mating, because the ratio of costs to benefits will likely influence the occurrence and extent of extra-pair mating.

We examined the influence of travel costs and body condition on extra-pair mating behavior in tree swallows (*Tachycineta bicolor*) by experimentally increasing the cost of travel for females. Tree swallows have one of the highest levels of extra-pair paternity in birds (Barber et al. 1996), with up to 89% of broods containing extra-pair young in our population (Whittingham and Dunn 2001). Females routinely travel >1 km from their nest box during their fertile period for both foraging and roosting (Dunn and Whittingham 2005). These long distance movements may also include extra-pair matings, as many extra-pair young are sired by males that are not resident in the study population (Dunn et al. 1994b; Whittingham et al. 2006). To examine the impact of travel costs and female condition on paternity, we clipped some flight feathers before egg-laying. Tree swallows are aerial insectivores, so clipping

flight feathers increases the cost of flight and leads to reduced body condition (mass corrected for size; Whittingham et al. 1994; Nooker et al. 2005). As a consequence, we predicted that handicapping females would lead to greater costs of finding an extra-pair mate and this would lead to less discriminating mate choice by females.

Materials and methods

Study area and species

We studied tree swallows in 2001 and 2002 at the University of Wisconsin-Milwaukee Field Station near Saukville, WI, USA (43°23' N, 88°01' W). Our study area contained 88 nest boxes with predator guards, located in two grids 600 m apart. Within grids, nest boxes were 40 m apart along a row and 28 m apart on the diagonal between rows. Tree swallows defend a small area around the nest box, but do not defend breeding or foraging territories (Robertson et al. 1992). In our population, tree swallows are socially monogamous and single-brooded. Females build a grass cup nest inside the nest box during late April and early May and begin egg-laying when the nest cup is 4–6 cm deep. They lay four to six eggs and begin incubation (14–15 days) with the penultimate egg; only the female incubates (Robertson et al. 1992).

All adults were caught inside nest boxes; they were measured (wing chord and tarsus length), weighed, and marked with a numbered aluminum band on the right leg and a colored plastic band on the left leg. Body condition was estimated from the residuals of the regression of body mass on tarsus length (Nooker et al. 2005). Females were classified as second-year (SY) or after second-year (ASY) on the basis of plumage coloration (Hussell 1983), and only ASY females were used in the experiment. Adults were marked on their breast or wings with nontoxic felt tip markers or acrylic paint to identify individuals in the field. We checked nest boxes every other day during the nest building period and daily when the height of the nest cup reached 3 cm through day 12 of the nestling period. On day 12, we weighed and measured nestlings and collected a small (50 μ l) blood sample for molecular analyses (see below). Blood samples were stored in lysis buffer at 4°C. Unhatched eggs and dead nestlings were collected and tissues were frozen at -20°C.

Feather clipping experiment

In 2001 and 2002, we conducted an experimental study of the effect of female body condition and foraging ability on reproductive performance (Nooker et al. 2005) and brood sex ratio (Whittingham et al. 2005). Details of our

experiment are presented in Nooker et al. (2005). Briefly, experimental females had three primaries on each wing (numbers three, five, and seven counting from the innermost primary feather outward) and four central tail feathers clipped at the base of each feather when nests had at least 3 cm of nest material. On average, handicapped females were clipped 20 days (± 1.1) before they started laying. At the time of initial capture, there was no difference in body condition between experimental and control females (Nooker et al. 2005). Previous feather clipping experiments have been conducted on male (Whittingham et al. 1994) and female (Winkler and Allen 1995) tree swallows with no significant effect on fledging success (Nooker et al. 2005). Clipped feathers are replaced during molt in July and August, so the effects of this treatment are short-term. Females were recaptured and weighed on the second day of incubation and, again, when nestlings were 4 days old. Experimental females lost 5.5% of their body mass by the second day of incubation, while control females gained 1.5% of their body mass (Nooker et al. 2005).

Paternity analysis

Paternity was determined from analysis of allelic variation at eight microsatellite loci (for more details, see Whittingham et al. 2006). The microsatellite primers we used were designed for tree swallows and several other species of birds and included: HrU6, HrU7 (Primmer et al. 1995), IBI 5-29 (Crossman 1996), TBI-81 and TBI-104, (Stenzler 2001), Pca3 (Dawson et al. 2000), LTR6 (McDonald and Potts 1994), and Ppi2 (Martinez et al. 1999). These microsatellite loci were highly polymorphic and had a combined exclusion probability (P_{ex}) of 0.9996 (Whittingham et al. 2006).

We genotyped breeding pairs and their young from 26 experimental and 23 control broods, which included 98 adults and 217 young from 231 eggs (94%). We did not obtain DNA from 14 eggs that showed no embryonic development. We also genotyped 80 additional males that were resident on our study area during 2001–2002. All individuals were genotyped at four loci (HrU6, LTR6, TBI-81 and TBI-104) and the combined probability of paternal exclusion (P_{ex}) was 0.996. All young matched their putative mother at all four loci. Nestlings were considered within-pair young if they matched the putative father at all four loci and extra-pair young if they mismatched the putative father at two or more loci. There were two young that mismatched their putative father at only one locus. These young and their putative father were genotyped at four additional loci (Pca3, HrU7, Ppi2 and IBI 5-29); in both cases, these young mismatched the putative father at two or more loci after the additional genotyping. To assign extra-pair sires, the paternal alleles of the extra-pair young

were compared to the alleles of all males in the population at all four loci. Extra-pair sires were assigned only when they matched an extra-pair young at all four loci ($n=60$ young). The probability that a randomly chosen male would match an extra-pair nestling at all four loci ranged from 1×10^{-5} to 0.0133 (mean \pm SD, 0.0018 ± 0.0028). There were seven extra-pair young that matched two potential extra-pair sires at all four loci. These individuals were also genotyped at four additional loci (see above) to determine the actual extra-pair sire. These seven young matched only one extra-pair sire at all eight loci.

In 13 nests, there were at least two extra-pair young with unknown sires. In these cases, we estimated the number of extra-pair sires by estimating the number of full- and half-siblings in the brood with the computer program Kinship 1.2 (Goodnight and Queller 1999). For each pairwise comparison of nestlings, Kinship used a simulation routine to test the primary hypothesis that the two nestlings were full siblings.

Data analysis

Distance measures between the female's nest box and the extra-pair sire's nest box were log-transformed to achieve normality. Means are presented with their standard errors (\pm SE), and all tests were two-tailed unless noted otherwise. Sample sizes vary because it was not possible to collect data on all variables for all individuals. The proportion of extra-pair young was not normally distributed, so we analyzed it using generalized linear models (GLM) with binomial errors and logit links as implemented in the program GLMstat (Beath 1997). This analysis used the number of extra-pair young in each brood as the dependent (response) variable and brood size as the binomial denominator.

Results

Handicapped (85%, 22/26 nests) and control (70%, 16/23 nests) females were equally likely to have extra-pair young in their nests (Fisher's exact test, $P=0.31$), and among females with extra-pair young, there was also no difference between handicapped ($63 \pm 5\%$) and control ($59 \pm 7\%$) females in the proportion of extra-pair young in the brood ($GLM \chi_1^2 = 0.2$, $P = 0.68$). Handicapped females started egg-laying later (28 May \pm 1.4 days) than control females (23 May \pm 1.6 days; $t_{47}=2.3$, $P=0.027$), but the proportion of extra-pair young was not related to laying date for either control ($GLM \chi_1^2 = 0.01$, $P = 0.79$) or handicapped females ($GLM \chi_1^2 = 1.8$, $P = 0.17$).

Over half of the extra-pair young (55%, 56/102) in our study were sired by resident males breeding in nest boxes

($n=30$ males siring one to four young). An additional 15 extra-pair young (15%, 15/102) were sired by seven floater males (caught at nest boxes but not known to breed), and the remainder were sired by unknown males. Using both these assigned extra-pair sires and relatedness estimates between unassigned extra-pair nestlings (see “Materials and methods”), we were able to estimate the total number of extra-pair sires in every nest. The number of extra-pair sires in a brood did not differ between handicapped (1.8 ± 0.2 extra-pair sires per brood, $n=22$) and control (1.8 ± 0.2 extra-pair sires per brood, $n=16$) females ($t_{36}=0.20$, $P=0.84$). Results were similar when we excluded the 12 nests with estimates of the number of sires based on nestling relatedness (handicapped females, 1.6 ± 0.2 extra-pair sires per brood, $n=16$; control females, 1.9 ± 0.3 extra-pair sires per brood, $n=10$; $t_{24}=0.74$, $P=0.47$).

The handicapping experiment did not have a significant influence on the level of extra-pair mating (proportion of extra-pair young or number of sires), but it did affect the spatial distribution of extra-pair mating at two levels. First, among females with extra-pair young, handicapped females were more likely to have an extra-pair sire that was resident on the nest box grid (82%, 18/22) than were control females (44%, 7/16; $\chi^2_1 = 6.0$, $P = 0.01$). Second, among known extra-pair sires that were resident on the nest box grids, the mean distance between nest boxes of females and their extra-pair sires was shorter for handicapped (86 ± 17 m, $n=18$) than control females (216 ± 50 m, $n=7$; t using ln-transformed data = 2.7, $df=23$, $P=0.01$). In this analysis, we used the average distance to the nests of extra-pair sires when there was more than one extra-pair sire at a nest.

Lastly, we examined the morphology of known extra-pair sires (residents and floaters) to determine if handicapped females mated with males that had smaller and more variable traits than control females. There was no difference in mean body mass ($t_{23}=0.13$, $P=0.90$) or tarsus length ($t_{21}=0.73$, $P=0.73$) between extra-pair sires at nests of handicapped and control females (average values were used when there was more than one extra-pair male). However, extra-pair sires were more variable in tarsus length at the nests of handicapped (0.39 SD) than control (0.16 SD) females (Bartlett $F_1=4.25$, $P=0.04$). There was no difference in the variance of body mass (Bartlett $F_1=0.01$, $P=0.93$).

Discussion

Our handicapping experiment increased the cost of travel for females and resulted in a decrease in the distance to extra-pair sires (a change in spatial distribution), but no change in the level of extra-pair fertilization. Many other studies of extra-pair paternity have examined and failed to

find ecological correlates of extra-pair paternity, but they have generally not identified sires and, thus, have not been able to determine if the spatial distribution of sires is correlated with ecological factors such as density or synchrony. Mate choice studies, primarily in the laboratory, have manipulated the costs of choosing mates through changes in food (Hunt et al. 2005), or parasite (Hedrick and Dill 1993) abundance, or the energetic cost of travel (Milinski and Bakker 1992; Wong and Jennions 2003) and found that mating preferences change. In most cases, increasing the cost of travel or searching for mates has decreased the relative benefits of mate choice and resulted in less choosy females. Female tree swallows also appeared to be less choosy when handicapped, because they chose extra-pair mates that were closer to their nest box and more variable in body size (tarsus length). This change in the distribution of extra-pair sires is unlikely to be due to greater male coercion of handicapped females, because handicapped females did not have more extra-pair sires or extra-pair young than control females. Despite an obvious increase in search costs, handicapped females maintained a high level of extra-pair mating (85% had extra-pair young), which suggests that it provides a significant benefit to females.

One other study has examined how handicapping influences the patterns of extra-pair paternity. In pied flycatchers (*Ficedula hypoleuca*), Ellegren et al. (1995) handicapped males because extra-pair copulations were only seen when males visited females on other territories, and they were primarily interested in how male attractiveness influenced paternity. Ellegren et al. (1995) expected that females paired with handicapped males would be more likely to engage in extra-pair copulations when neighboring males visited them. Their experiment could also be seen as increasing the cost of gaining extra-pair copulations by handicapped males. In any case, the level of extra-pair paternity did not differ between handicapped and control males, although the sample size was small ($n=9$ handicapped males; Ellegren et al. 1995). It is possible that the spatial pattern of paternity could have changed in pied flycatchers, as it did in tree swallows, but was undetected by Ellegren et al. (1995). This study raises the issue of which sex initiates extra-pair copulations and how experimental manipulations influence the mating behavior of each sex.

There are several possible interpretations of our results, depending primarily on whether females choose extra-pair mates. First, handicapped females may have been less discriminating in their choice of extra-pair mates, as found in other studies that have increased search costs. Second, female tree swallows may not have any strong mate preferences, and the change in spatial distribution of paternity may simply reflect a higher encounter rate between handicapped females and nearby males. Lastly, if

males coerce extra-pair copulations, then extra-pair males near handicapped females may have coerced them into copulating more often than control females, or handicapped females may have had lower “resistance” to these attempts (Arnqvist and Kirkpatrick 2005). We argue below that these second and third interpretations are unlikely given our knowledge of tree swallow mating behavior.

It is clear that female tree swallows have mating preferences and do not engage in extra-pair mating indiscriminately. In a paired comparison, Kempenaers et al. (2001) found that extra-pair males had fewer parasites (as indexed by holes in flight feathers), weighed more, and were in better body condition than the males they cuckolded. Behavioral evidence also suggests that tree swallows do not mate indiscriminately with extra-pair males, as 54% of extra-pair copulations are refused, and extra-pair copulations were more likely to be successful (result in cloacal contact) when initiated by females than males (Venier et al. 1993). Weak mating preferences are also not consistent with experimental evidence that females exert significant control over which males fertilize their clutch (Lifjeld and Robertson 1992). It is also unlikely that females are harassed or coerced into copulating, as females are not pursued by males away from their nest, and at their nest they refuse copulation attempts simply by keeping their tail down (Venier et al. 1993; personal observation by Dunn and Whittingham, unpublished data). However, future studies should examine the copulation behavior of handicapped females to determine if they incur greater sexual harassment by males. If coercion did occur, then we would expect the level of extra-pair fertilization (percentage of nests or young, number of extra-pair sires) to be greater for handicapped than control females, but this did not occur. Furthermore, if male coercion were common, we would expect to see the same males siring young in successive broods (i.e., paternity should be repeatable), but this did not occur in an experimental study in which two clutches were laid in quick succession (Whittingham et al. 2006). Thus, we suggest that handicapping did not simply allow males greater copulatory access to handicapped females. Instead, handicapping made it more costly for females to fly and this probably affected female mate searching behavior, both locally (among resident males) and farther away (outside the nest box grids). Female tree swallows may be unusual among passerines, as they travel long distances from their nest box each day during the fertile period (up to 10 km for foraging and roosting; Dunn and Whittingham 2005) and often engage in extra-pair matings with males that are not local residents (45% of extra-pair young in this study; Dunn et al. 1994a; Kempenaers et al. 2001; Dunn and Whittingham 2005).

Despite the higher costs of travel, handicapped females continued to gain extra-pair fertilizations at the same level

as control females, which suggests that the indirect benefits of extra-pair mating are significant. Only the spatial distribution of mates changed; if the benefits of extra-pair mating were minor, we would have expected lower levels of extra-pair fertilization, rather than just a change in the spatial pattern of mating. Some authors have claimed that the indirect benefits of choosing males with superior genotypes are likely to be small and, thus, unlikely to offset the large direct costs of mate sampling (Arnqvist and Kirkpatrick 2005). Few studies have examined this question directly. Some have found that searching for mates has a relatively low energetic cost, which implies that the indirect benefits do not need to be large to maintain female choice for male genes (Gibson and Bachman 1992), while others have found that the energetic costs of mate sampling are substantial, suggesting that indirect benefits need to be large (Byers et al. 2005). Further empirical studies of the cost of mate choice are needed to help resolve this issue.

Clipping flight feathers led to an immediate increase in the flight costs of female swallows, and by the beginning of incubation, it also led to a 7% reduction in body condition relative to control females (Nooker et al. 2005). Numerous studies have found that female mate choice shows behavioral plasticity in relation to female body condition or parasitism. Most studies have found that poor condition or parasitism decreases female choosiness (reviewed by Hunt et al. 2005), although others have not (Zuk et al. 1998; Buchholz 2004). Reduced female choosiness could occur as a consequence of an adaptive reallocation of resources or simply a debilitating effect on the ability of females to find and discriminate among potential mates. In either case, females in poorer condition might be less choosy and mate with a broader range of male phenotypes, which could lead to a decrease in the intensity of sexual selection (see “Introduction”). We found that extra-pair sires of handicapped females were more variable in tarsus length than those of control females, which is consistent with less discriminating mate choice by females. It is not clear, however, if female tree swallows choose extra-pair mates based on tarsus size. Kempenaers et al. (2001) found that body mass, but not tarsus or wing length, was greater among extra-pair than within-pair males; however, in our population body mass is correlated with both tarsus and wing length (unpublished data).

One implication of our study is that an important source of selection may have been overlooked by previous studies that examined only the proportion of extra-pair young or broods. For example, studies that manipulated the availability of mates (e.g., through changes in density or synchrony) may not have found a change in the level of extra-pair paternity, but they could have changed the spatial distribution of males gaining extra-pair paternity (as in this study). For example, a decrease in density could increase

search costs and result in a reduction in the distance between females and their extra-pair mates. As a result, more males in the population will gain extra-pair matings, and there is likely to be weaker sexual selection on male traits. These effects could remain undetected unless researchers identify extra-pair sires.

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