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Radio-tracking of female Tree Swallows prior to egg-laying

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ABSTRACT. We radio-tracked eight female Tree Swallows (*Tachycineta bicolor*) prior to egg-laying in 2000 and 2001. Six females made movements >2 km to evening roosting sites. Females often roosted farther away than the nearest available roost site, they used different roosts on different nights, and during the day they foraged up to 10 km from their nest site. Thus, female swallows move over a large area (103 km^2) prior to egg-laying. These widespread movements appear to be unusual among swallows, and they may allow females to survey a large number of extra-pair males.

SINOPSIS. **El uso de radiotelemetría para estudiar individuos de *Tachycineta bicolor* previo al periodo de puesta de huevos**

Durante 2000 y 2001, le colocamos radiotransmisores a ocho hembras de *Tachycineta bicolor* previo a la época de puesta. Seis machos se desplazaron mas de 2 km a lugares para pernoctar. Las hembras pernoctaron mucho mas lejos que los lugares disponibles, y usaron una localidad diferente cada noche, y durante el día forrajearon a distancias que quedaban a 10 km del lugar de anidamiento. Por lo tanto, las hembras de esta golondrina se desplazan sobre áreas de gran dimención (103 km^2) previo a poner. Estos movimientos tan amplios parecen ser poco usuales entre las golondrinas, y pudieran permitirle a las hembras examinar a otros machos que no sean su pareja, para copular con estos.

Key words: extra-pair paternity, foraging, radio-tracking, *Tachycineta bicolor*

Tree Swallows (*Tachycineta bicolor*) have one of the highest known levels of extra-pair fertilization among socially monogamous birds. The percentage of broods containing at least one extra-pair young ranges from 50 to 89% depending on location and year (Barber et al. 1996; Dunn et al. 1994; Kempenaers et al. 1999, 2001; Whittingham and Dunn 2001). Studies of extra-pair mating in passerines generally reveal that the sires of extra-pair young are males within a few territories of the young (e.g., Thusius et al. 2001; Webster et al. 2001). In contrast, several studies of Tree Swallows have revealed that 80% of the sires of extra-pair young are not nearby residents (Dunn et al. 1994; Kempenaers et al. 1999). Although extra-pair fertilizations occur in most broods of Tree Swallows, extra-pair copulations are rarely seen at the nests of females (4% of all successful copulations; Venier et al. 1993). This suggests that extra-pair copulations occur primarily when females are away from their nest.

In this study we used radio-telemetry to determine how far females move from their nest sites during their fertile period and where they go to roost. We focused on movements to roost sites because most copulations, including extra-pair copulations, are thought to occur early in the morning (Venier and Robertson 1991), and, thus, roost sites might be locations where individuals from a large area can engage in extra-pair mating. We also present novel observations of long-range foraging behavior and low fidelity of individuals to the same roost site. Previous observations of radio-tagged swallows suggest that once birds settle at a nest site they generally forage close by and become more restricted in their choice of roost site (Alves and Johnstone 1994; Brown and Brown 1996).

METHODS

Tree Swallows are secondary cavity nesters that readily accept nest boxes. We followed radio-marked Tree Swallows during 2000 and 2001 at the University of Wisconsin-Milwaukee Field Station, southeast of Newburg, Wisconsin (43°23′N, 88°01′W). Over 80 nest box-

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es for Tree Swallows have been in place since 1997. Nest boxes were arranged in two grids with additional "solitary" boxes scattered between the grids. The two grids consisted of 27 to 46 nest boxes each (depending on the year), arranged in rows that were 40 m apart with the nearest diagonal neighbor 28 m away. Surveys were conducted every two to three days to identify social mates and to record the progress of nest building. Nests near completion (>4–5 cm grass cup) were checked daily for the first egg.

Females with nests nearing completion were caught inside nest boxes. We used only newly caught adult females in this study. Each bird was given a uniquely numbered USFWS aluminum leg band and a single plastic leg band. Age (yearling or older than one year) and sex were determined using plumage characteristics and wing chord, as well as the presence of a cloacal protuberance (Hussell 1983). We attached radio transmitters (BD-2A, Holohil Systems Ltd., Carp, Ontario) to eight females from 5–17 May. Transmitters weighed 0.75 g and were approximately 3.6% of total body mass. Six females nested within the same grid of nest boxes (within 200 m of each other) and the other two females nested in solitary boxes up to 400 m away. Transmitters were glued to the upper back of birds between the wings using Skin-Bond latex cement (Smith and Nephew, Andover, MA) as recommended by Holohil Systems Ltd. (see Brown and Brown 1996). We parted feathers to expose a small area of skin and then gently pressed the transmitter (with glue on the bottom) against the skin and held the transmitter in place for 5–10 min before releasing the bird.

We monitored birds at least every hour in the early morning (05:00–07:00) and afternoon (14:00–18:00) before intensive tracking (locations taken every 30 min) in the evening (18:00–20:30) to locate roost sites. During tracking, we used a car to follow birds, and we recorded their locations to the nearest 100 m based on visual observation or signal strength (e.g., when they entered inaccessible marshes at night). Every female we radio-marked was resident at the same nest box where she was caught originally.

RESULTS

Two of the radio transmitters fell off within one day of release. We obtained information about roosting locations or daily foraging activity from the remaining six females (1 to 14 d before laying) over 17 tracking days (range, 1–3 d per female). Four females were tracked to their roost site on at least two nights, and three of these females went to different roost sites on different nights. Of these three females (Fig. 1), one (936) roosted at three different locations over a period of four consecutive days (8–6 d before her first egg was laid), a second female (799a) roosted at two different locations over three consecutive days (7–5 d before laying), and the third female (799b) roosted in two different locations on three nights (14–10 d before laying). Two females were tracked to roost sites on only one night before the transmitter fell off or it was removed after the first egg was laid. Overall, the females in this study went in four general directions toward roost sites (Fig. 1). In most cases these roost sites could not be located precisely because the site was inaccessible at night. However, it was clear that females roosted at distant (>2 km) and different roost sites, even though they all nested in the same area.

Maximum transmitter range was about 1 km when birds were flying. In general, the pre-roosting behavior of birds involved foraging high in the air (at least 200 m above ground) for up to 1.5 h before roosting. Up to several hundred birds would forage in a loose group slowly moving in the direction of the roost, and, then, as it became dark (typically >20:15 CST), the birds would descend toward the roost. In the morning, birds started flying before it was light and made faster movements back to their nest boxes. Two females each traveled 2.2 and 3.3 km back to their nest boxes in <15 min (from Doughnut and Gough Lakes, respectively; Fig. 1).

Roost sites varied from large (Mud Lake is 99 h) to small (1 h) lakes and ponds (Fig. 1). Among our six birds, there was a total of 12 known roost-nights. Only a third of these (4 of 12) were from Mud Lake, the closest known roost site to the nesting area (Fig. 1). Another third of roost-nights occurred northeast of the study area, and the remainder were split evenly between northwest (2) and southwest (2) of the nesting area (Fig. 1). In most cases it was not possible to estimate the number of birds at a particular roost, but there were often 50–100 birds flying in a loose group before it became too dark to see. However, we were able to ob-

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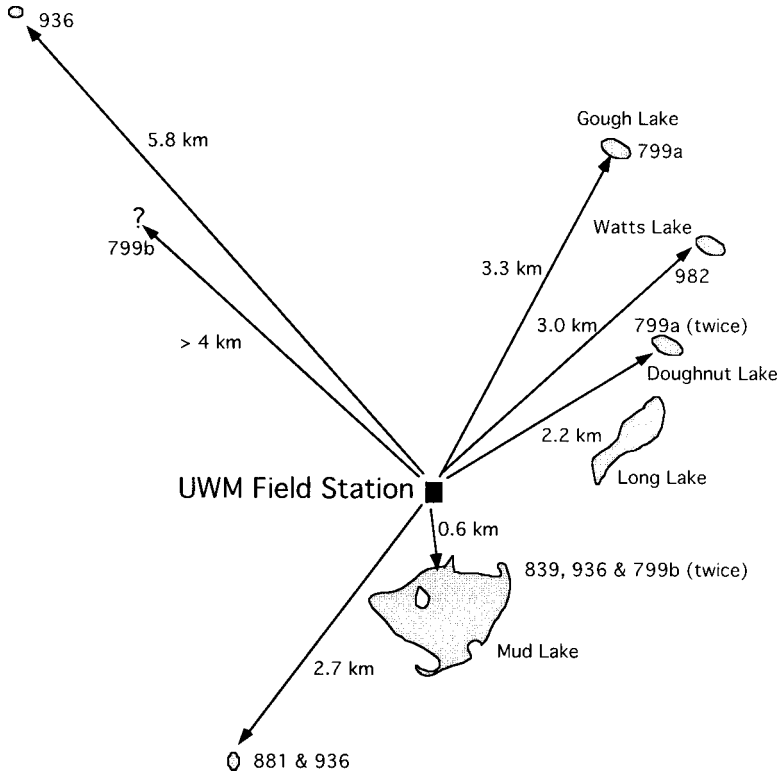

Fig. 1. Movements of radio-marked female Tree Swallows to roost sites near the UWM Field Station, 2000 and 2001. Individuals are indicated by their radio frequency. Arrows indicate straightline direction to roost sites. Question mark indicates location of roost was unknown and bird was lost at that approximate location.

serve one large roost containing several species. On the evenings of 15 and 16 May 2000, we observed several hundred Tree Swallows in a group of >10,000 swallows, mostly Bank Swallows (*Riparia riparia*) and Barn Swallows (*Hirundo rustica*), roosting in dense stands of cattail (*Typha* spp) at the edge of Mud Lake (Fig. 1). Two of our radio-marked birds roosted with these other species at Mud Lake on 15 May 2000.

Most females tended to stay near the nest box (within 0.5 km) during the day. However, on 20 May 2001 we continuously radio-tracked one female (982) for 3.5 h (14:00 to 17:35) as she traveled in a large circular route up to 10.2 km south of Mud Lake. This female appeared to be alone and in flight most of the time. Interestingly, after spending most of the afternoon south of her nest box, this female returned to her nest box at 17:35, left for her roost site at 18:27 and finally arrived at the roost site, which was 3.0 km north of her nest box at 19:15. The next morning she laid her first egg. Another female (936) was also found foraging a long distance from her nest box during the afternoon of 15 May 2001. This female was 5.8 km northwest of her nest box at 15:00, but in this case the female roosted nearby and did not return to her nest box until the next morning.

All eight females seemed to behave normally after a short period of adjustment to the radio transmitter. Most returned to their nest boxes within minutes of release and several were seen copulating normally with their mates. There was no sign of injury when birds were recaptured and examined ($N = 5$; typically 2–3 wks after the transmitter fell off), and all recaptured birds were within the normal range of body mass.

DISCUSSION

Prior to egg-laying, most female Tree Swallows stayed within 0.5 km of the nest box dur-

ing the day, but occasionally females left on extensive afternoon forays (>3 h and 10 km from the nest). Females roosted at sites up to 5.8 km away, in most cases farther than the nearest known roost site (Mud Lake), and individual females also went to different roosts on different nights. Overall, the females in this study, which all nested within 0.5 km of each other, chose roost sites over an area of at least 103 km^2. Hundreds of swallows roosted together at some of these sites, which suggests that females may have an opportunity to choose from a much larger pool of potential extra-pair mates at roost sites than at their nest site.

Two other studies have examined movements of radio-marked swallows during the breeding season. Radio-marked Cliff Swallows (*Petrochelidon pyrrhonota*) showed long distance movements (9–24 km) early in the breeding season, which were probably related to selection of a nesting colony (Brown and Brown 1996). Prior to settling at a colony, females moved farther than males (13.8 vs. 5.2 km), and females visited an average of 4.3 colonies (Brown and Brown 1996). These movements may allow females to gain some information about the ectoparasite load at a colony, which has significant fitness consequences. After settling to breed at a particular colony, female Cliff Swallows did not switch roost sites (Brown and Brown 1996). In contrast, Tree Swallows in this study regularly switched roost sites during nest-building. Thus, it does not seem likely that selection of roost sites in Tree Swallows is related to nest-site selection or avoidance of ectoparasites or biting midges (e.g., Davidar and Morton 1993). In a second study of radio-marked swallows, Alves and Johnstone (1994) tracked a pair of Bank Swallows in Scotland during the nestling period. The pair roosted together at four different sites over seven days (3–4.7 km from their nest).

It would be interesting to know if paired male and female Tree Swallows also roost at the same sites each night. We did not radio-track males, but in two cases we knew that in the morning the male arrived at the nest box 10 min before the female, suggesting that males are not closely following their mates from roosts to the nest box (assuming they go to the same roost).

Little is known about the roosting behavior of swallows during the breeding season. Most studies have examined the large communal roosts of birds during migration or in winter. In Arizona it appears that roost locations of Purple Martins (*Progne subis*) change seasonally (between May and August), but it is not known if the same individuals are switching roosts (Anderson and Anderson 1946). These Arizona roosts appeared to attract birds over a region of 1425 km^2, which is larger than the area traversed by Tree Swallows in this study (102 km^2). Radar studies of Purple Martin roosts have also indicated that birds fly long distances from the roost during each day (regularly 80 km away; Russell and Gauthreaux 1999). Prior to laying, Purple Martins regularly roost inside their nest houses, and often with their mate who likely copulates with the female inside the nesting compartment in the morning (Brown 1980). In contrast, Tree Swallows rarely roost inside their nest boxes at this stage, except during unusually cold weather (Stutchbury and Roberston 1990), and most within-pair copulations occur on top of the nest box in the morning after birds return from the roost (Venier and Roberston 1991; Dunn and Whittingham, unpubl. data). Further study is needed to determine if these differences in mating behavior between two ecologically similar species influences their roosting behavior (see Brown 1980).

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LITERATURE CITED

ALVES, M. A. S., AND I. G. JOHSTONE. 1994. Radio-tracking small aerial foraging birds: a preliminary study of the Sand Martin, *Riparia riparia*. Avocetta 18: 13–20.

ANDERSON, A. H., AND A. ANDERSON. 1946. Notes on the Purple Martin roost at Tucson, Arizona. Condor 48: 140–141.

BARBER, C. A., R. J. ROBERTSON, AND P. T. BOAG. 1996. The high frequency of extra-pair paternity in Tree Swallows is not an artifact of nestboxes. Behavioral Ecology and Sociobiology 38: 425–430.

BROWN, C. R. 1980. Sleeping behavior of Purple Martins. Condor 82: 170–175.

———, AND M. B. BROWN. 1996. Coloniality in the Cliff Swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, IL.

DAVIDAR, P., AND E. S. MORTON. 1993. Living with

FIELD ORNITHOLOGY
Tuesday May 10 2005 07:03 PM
Allen Press • DTPro System
GALLEY 264
forn 76_307 Mp_264
File # 07TQ

parasites: prevalence of a blood parasite and its effect on survivorship in the Purple Martin. Auk 110: 109–116.

DUNN, P. O., R. J. ROBERSTON, D. MICHAUD-FREEMAN, AND P. T. BOAG. 1994. Extra-pair paternity in Tree Swallows: why do females mate with more than one male? Behavioral Ecology and Sociobiology 35: 273–281.

HUSSELL, D. J. T. 1983. Age and plumage color in female Tree Swallows. Journal of Field Ornithology 54: 312–318.

KEMPENAERS, B., B. CONGDON, P. T. BOAG, AND R. J. ROBERTSON. 1999. Extra-pair paternity and egg hatchability in the Tree Swallows: evidence for the genetic compatibility hypothesis? Behavioral Ecology 10: 304–311.

———, S. EVERDING, C. BISHOP, P. T. BOAG, AND R. J. ROBERTSON. 2001. Extra-pair paternity and the reproductive role of male floaters in the Tree Swallow (*Tachycineta bicolor*). Behavioral Ecology and Sociobiology 49: 251–259.

RUSSELL, K. R., AND S. A. GAUTHREAUX, JR. 1999. Spatial and temporal dynamices of a Purple Martin pre-migratory roost. Wilson Bulletin 111: 354–362.

STUTCHBURY, B. J., AND R. J. ROBERTSON. 1990. Do Tree Swallows use nest cavities as night roosts during territory establishment? Journal of Field Ornithology 61: 26–33.

THUSIUS, K., K. PETERSON, P. O. DUNN, AND L. A. WHITTINGHAM. 2001. Male mask size is correlated with mating success in the Common Yellowthroat. Animal Behaviour 62: 435–446.

VENIER, L. A., AND R. J. ROBERTSON. 1991. Copulation behaviour of the Tree Swallow, *Tachycineta bicolor*: paternity assurance in the presence of sperm competition. Animal Behaviour 42: 939–948.

VENIER, L. A., P. O. DUNN, J. T. LIFJELD, AND R. J. ROBERTSON. 1993. Behavioural patterns of extra-pair copulation in Tree Swallows. Animal Behaviour 45: 412–415.

WEBSTER, M. S., H. C. CHUANG DOBBS, AND R. T. HOLMES. 2001. Microsatellite identification of extrapair sires in a socially monogamous warbler. Behavioral Ecology 12: 439–446.

WHITTINGHAM, L. A., AND P. O. DUNN. 2001. Survival of extrapair and within-pair young in Tree Swallows. Behavioral Ecology 12: 496–500.