J. Field Ornithol. 75(4):353–358, 2004

Breeding between Tree Swallows from the same brood

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Received 26 September 2002; accepted 6 February 2004

ABSTRACT. We provide data on three instances where Tree Swallows (*Tachycineta bicolor*) that fledged from the same nest (broodmates) eventually bred together in subsequent years. Two instances were detected in Ontario and a third was detected in Nova Scotia. Based on demographics at the times of each event, we estimated probabilities of these broodmate pairings as approximately 1 in 16,000, 1 in 5600, and 1 in 29,000, respectively, whereas the number of identified pairs in the populations was less than 65 in each case. Thus, inbreeding occurred at a higher frequency than expected by chance. We cannot distinguish whether these identical natal dispersal responses arose from similarity in genes or in rearing environments.

SINOPSIS. **Reproducción entre individuos de *Tachycineta bicolor* de la misma camada**
En este trabajo proveemos datos, de tres ocasiones, en donde individuos de la golondrina *Tachycineta bicolor*, de la misma camada, se aparearon y se reprodujeron. Se detectaron dos casos en Ontario y un tercero en Nova Scotia. Basados en datos demográficos al tiempo de cada evento, estimamos la probabilidad de apariamiento de individuos de la misma camada de l en 16,000, y de l en 5600 y de l en 29,000, respectivamente. Cabe señalarse que el número de parejas identificadas en la poblacion fue menor a 65 en cada caso. Por lo tanto la endogamia en esta especie ocurrió en una frecuencia mayor a la esperada por probabilidad. No pudimos distinguir si la dispersión identical de hermanos responde a similaridad en los genes o al ambiente en donde se crian.

Key words: dispersal, inbreeding, mate choice, *Tachycineta bicolor*, Tree Swallow

Although limited inbreeding can be a beneficial mating strategy for maintaining local adaptations (Shields 1982; Bateson 1983; Hewitt and Butlin 1997; Bensch et al. 1998), close inbreeding can have substantial fitness costs (e.g., McRae 1996; Brown and Brown 1998; Keller 1998). In many species, close inbreeding is unlikely because natal dispersal (movements between site of birth and site of first breeding) lowers the probabilities that relatives will encounter each other the farther they move from their natal site (Weatherhead and Forbes 1994; Clobert et al. 2001; Shutler and Clark 2003). This probability is further reduced by mortality, which in some small passerines may be 75% before breeding age is attained (Shutler and Clark 2003). Thus fitness costs, dispersal, and demographics combine to make close inbreeding rare for a variety of taxa (Pusey 1987; but see Duarte et al. 2003). Herein we report three cases in which former broodmate Tree Swallows (*Tachycineta bicolor*) bred together. We distinguish broodmates from sibs because high rates of extra-pair paternity in this species (e.g., Lifjeld et al. 1993) mean that individuals in the events we describe may not have been full sibs. We estimate probabilities for these events, assess whether inbreeding resulted in unhealthy offspring, and speculate on reasons such events occurred.

STUDY AREAS AND METHODS

The Long Point Bird Observatory (LPBO) grids are at four sites near Port Rowan, Ontario, Canada (42°37′N, 80°27′W): Long Point (LP) is 1 km from the eastern tip of the Long Point peninsula in Lake Erie, Sewage Lagoons (SL) is at Port Rowan's waste treatment ponds, 33 km west of LP and about 0.5 km west of the village, Backus Field (BF) is 3.3 km north-north-

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west of Port Rowan in the Backus Conservation Area, and Mud Creek (MC) is 1 km east of BF. Nest boxes at LP, BF, and SL were initially occupied by Tree Swallows beginning in 1969, 1976 and 1977, respectively. In 1987, the BF nest boxes were moved to MC. Each site had 10–160 nest boxes available each year (mean = 68.9, N = 81 site-years from 1969 to 2000). Most boxes were 24 m apart in lines or grids, but some were spaced more closely for experimental purposes.

The Leonard-Horn study area (L-H grid) is centered near 45°4′N, 64°20′W in the Gaspereau Valley of Nova Scotia, Canada, and consists of three orchards and an open field with a total of 115 nest boxes at least 5 m apart. Tree swallows have bred in this grid since 1988 (Garron 1989).

The Shutler study area (S grid) was initiated in 2000 and consisted in that year of seven orchards and a total of 150 boxes at least 25 m apart, centered about 2 km further north of the L-H grid, but including orchards east and west of the L-H grid in the Annapolis Valley of Nova Scotia. Minimum distance between the L-H and S grids was 3.8 km.

On all grids, boxes were 1.5 m above the ground, and were checked frequently in each year for breeding activity. Adults were captured opportunistically or trapped inside boxes usually after the eggs hatched (Magnusson 1984; Stutchbury and Robertson 1986). Adults were sexed by the presence of a brood patch (female) or cloacal protuberance (male), and banded if not already so. More than 60% of adults were banded each year for all grids, but some adults were not captured due to nest predation before hatching or for other reasons. No pairs were individually identified at the LP grid in 1973 or 1974. On all grids, all nestlings were banded, usually at 12 d of age.

LPBO band and box data were entered into a database by DL who subsequently searched for pairings between broodmates, between members of the same nestling cohort, and between returning nestlings and any other Tree Swallow. Inbreeding was not detected in a similar data base for the L-H grid. Inbreeding on the S grid was detected by similarity in band numbers of adults within a box that was traced to broodmates from the L-H grid.

The number of possible twosomes formed from a brood of i nestlings is $(i - 1) + (i - 2) + (i - 3) + \ldots + 3 + 2 + 1$, which is equal to $i(i - 1)/2$. Assuming an even sex ratio, half of those twosomes will be male-female pairs, so the number of possible broodmate pairs is $i(i - 1)/4$. Therefore the number of broodmate pairs from a population with a variable number of broods of several sizes is $\Sigma^{I}_{i=1}[N_i \cdot i(i - 1)/4]$, where i is brood size, N_i is the number of broods of size i, and I is the maximum observed brood size. Following similar logic, the number of possible cohort-cohort pairings from a site is $x\ (x - 1)/4$, where x is the number of nestlings banded at the site. The probability of broodmate pairing is the number of possible broodmate pairings divided by the number of possible cohort-cohort pairings. This is also the probability that a male and female sampled at random from a cohort would turn out to be broodmates. With respect to pairing, however, the opportunity to mate with Tree Swallows raised elsewhere or within a grid in other years, and survival, dilute the probability of cohort-cohort or broodmate pairings. To account for these factors, we also calculated the number of potential cohort pairs among all identified pairs on a grid (Table 1; we show fewer decimals than were used in calculations).

RESULTS

We found evidence of two broodmate pairings from LPBO and one from the joint L-H and S grids (Table 1).

In Ontario event 1, two nestlings from a brood of four, banded on 29 June 1976 in box 8 at BF, were captured as adults on 8 June 1978 attending a hatching brood in box 22 at SL. The latter nest box was about 3.0 km south of the natal box at BF. In SL box 22, a clutch of six was initiated on 21 May and completed on 26 May. Five of the six eggs hatched. Body mass and measurements of the outer primaries on 20 and 24 June indicated normal growth of the young (Zach and Mayoh 1982), which fledged some time between 27 June and 2 July. The female from this pair returned and bred again, with another male, in SL box 22 in 1979, but none of her 1978 young or her broodmate male were seen again. In 1976, 55 nestlings fledged from 12 broods on the BF grid (Table 1; mean, 4.6, range, 2–6). The 1978 broodmate pair involved the only two 1976 BF nestlings among all identified pairs at

Table 1. Probability calculations for each of the broodmate pairings observed among Tree Swallows.

Brood sizes from year producing broodmate pairings	Number of broods in preceding year		
	Ontario 1	Ontario 2	Nova Scotia
1		2	
2	1	2	3
3	0	3	6
4	3	5	7
5	7	21	16
6	1	31	12
7		2	5
a. Total possible broodmate pairings (see text for formula)	52.0	379.0	254.0
b. Total possible cohort pairings	742.5	28815.0	14220.5
c. Probability of any broodmates pairing (a/b)	0.07	0.01	0.02
d. Identified local pairs at time of incest	34	61	23
e. Number of identified female nestlings from cohort present	1	5	1
f. Number of identified male nestlings from cohort present	1	10	1
g. Possible number of cohort pairings (e *f)	1	50	1
h. Probability of cohort pairing (g/d^2)	0.0009	0.01	0.002
i. Probability of broodmates pairing among all breeders (c *h)	0.00006	0.0002	0.00003

SL in 1978. The joint probability of a pairing among returning nestlings and of that pairing being between broodmates was 1 in 16,044 (Table 1).

In Ontario event 2, two nestlings from a brood of five, banded on 26 June 1985 in box 13G at LP, were captured as adults attending a brood of six in box 18F at LP on 12 June 1987. The distance between those two nest boxes was 124 m. One egg was found in box 18F on 16 May 1987, but it had disappeared by the next day. A new clutch was started on 22 May and eggs were laid daily until 28 May, but the fifth egg was accidentally broken by an observer, leaving a final clutch of six. Those eggs hatched on 11 June and the brood of six was in good condition when the nestlings were banded, weighed, and measured on 23 June. Two young disappeared, possibly taken by a predator, between 23 and 27 June. The remaining four nestlings, which were in the normal range of mass and feather growth, fledged on 30 June. None of this brood, or the broodmate pair that attended them, was found again in subsequent years. In 1985, 340 banded nestlings fledged from 66 broods on the LP grid (Table 1; mean, 5.2, range, 1–7). All 65 breeding females and 61 of the breeding males on the LP grid were captured in 1987. The joint probability of a pairing among returning nestlings and of that pairing being between broodmates was 1 in 5658 (Table 1).

In Nova Scotia, on 5 June 2000, a second-year female was captured inside box 94 on the S grid. She had been banded in 1999 as a nestling in a brood of five on the L-H grid, a natal dispersal distance of 5.7 km (determined with a global positioning system unit accurate to within 6 m). Her clutch of five eggs hatched on 23 or 24 June. On 29 June we recaptured her and a male from her natal brood; the rapid detection of this pairing enabled us to collect more observational data than for the preceding pairings. Five nestlings were banded in box 94 on 4 July 2000; two of these apparently starved to death before we returned on 7 July, and a runt appeared emaciated. With the exception of the runt, and including the two dead nestlings, tarsus length, head length, wing length, tail length, and mass were within the normal range

for other Tree Swallow nestlings. We did not see evidence of superficial developmental abnormalities in any of the nestlings. On 14 July, we found wings and tarsi of one of the nestlings (estimated at 18–19 d old based on feather development) on the ground below the box, and two dead nestlings in the box (one also 18–19 d old and the runt in roughly the same stage of development as on 8 July). Clearly the nestling on the ground had been claimed by a predator, and presumably this explained the death of one nestling in the box; the runt had probably starved. In comparison in 2000, out of 16 other broods on the S grid that made it to 12 d of age or more, four other nestlings in three different nests were found starved to death. In any case, none of this brood successfully fledged. We were unable to recapture the male to more precisely quantify genetic relatedness among parents and offspring. However, we confirmed by observation that two adults were feeding at the nest on the morning of 7 July and on both the morning and afternoon of 8 July, although we could not identify those adults. Neither of the broodmates in this pairing has been seen since. In 1999, 242 banded nestlings fledged from 53 broods on the L-H grid (Table 1; mean, 4.6, range, 2–7). The joint probability of a pairing among returning nestlings and of that pairing being between broodmates in 2000 was 1 in 29,617 (Table 1).

DISCUSSION

The degree of inbreeding that occurred in these pairings is unknown, but published information on this species enables us to estimate its extent. Sib-sib breeding may not have occurred if intraspecific brood parasitism was responsible for making birds in these pairings broodmates, or if it accounted for the entire clutches at which these broodmates were captured. This is unlikely, however, because intraspecific brood parasitism occurs in less than 1% of Tree Swallow nests and even then, each female at the nest likely produces some of the eggs (Lombardo 1988; Lifjeld et al. 1993). Close inbreeding may not have occurred if one of the captured adult broodmates was a floater entering the nest for reasons other than tending its own brood (Lombardo 1987). However, floaters are far less likely to be captured in boxes than are breeders (Shutler and Clark 2003) presumably because they have less invested in the nest, and floaters are only commonly seen later in brood development than when we captured adults (M. Smith, J. Carr, D. Shutler, and D. Stewart, unpubl. data). A more likely factor influencing the extent of inbreeding is that broodmates may have been half rather than full sibs if either of them had been sired by a non-pair male (e.g., Lifjeld et al. 1993; Dunn et al. 1994; Barber et al. 1996). Similarly, the brood that the broodmates produced may not have been entirely inbred if a non-pair male had fertilized some of the eggs. Assuming that proportions of extra-pair young from Ontario are representative of all our study grids (population density probably does not influence rates of extra-pair paternity [Dunn et al. 1994; Conrad et al. 2001; Rätti et al. 2001]), there is roughly a 40% chance that broodmates will be half rather than full sibs, and roughly an 81% chance that some of the broodmate-produced broods were not inbred (Lifjeld et al. 1993). In any case, some inbred nestlings were likely in each of the nests.

Shutler and Clark (2003) found that broodmate Tree Swallows were significantly over-represented among natal returns to a Saskatchewan grid (also see Morton 1992; Brown and Brown 1996; van der Jeugd et al. 2002). (Nonetheless, none of over 1000 pairings in the Saskatchewan population involved former broodmates.) Similarity in natal dispersal behavior may relate to genes, from being raised in a common environment, or likely a combination of these two (Greenwood et al. 1979; Fleischer et al. 1984; Oring and Lank 1984; Johnson and Gaines 1990; Brown and Brown 1992). If similarity in natal dispersal is responsible for these pairings, we can only speculate on the proximate mechanisms that led to precisely equivalent natal philopatry. Did they migrate together? Were their homing instincts precisely and equally displaced? In any case, costs of inbreeding may select against such pairings. A delay in breeding date may suggest that these broodmates attempted to avoid mating with each other. However, in Ontario event 1, SL 22 initiated on 21 May 1978, four days after the 10th percentile (18 May) and three days before the median (24 May) for $\geq$ 2-yr old females (excluding repeat clutches in the same box) at that site in that year (N = 21). In Ontario event 2, LP 18F initiated on 22 May 1987, two days after the

10th percentile (20 May) and one day before the median (23 May) for ≥ 2-yr old females at that site in that year ($N = 59$). In Nova Scotia on the S grid in 2000, nine initiations occurred before, four on the same day, and five after the broodmate pair, and second-year females tend to initiate nests later than older birds anyway (Stutchbury and Robertson 1988). Thus, there was no sign of unusually late nesting by broodmate pairs. Although some nestlings from these broods did not fledge, we have no evidence that this was a consequence of inbreeding. Most eggs hatched (Koenig 1982; Kempenaers et al. 1996), and parental negligence and predators appeared to be the causes of their demise.

Within the population of banded adults, we have likely underestimated the frequency of broodmate pairings because many captured pairs consisted of two individuals whose natal origins were unknown, and some of these pairs could have involved broodmates. At the Ontario sites, the proportion of sib-sib pairings found among all known pairs (2/3120) indicates that the probability of detecting such a pairing at those sites was 1 in 1555 (among pairs in which both adults were captured). The proportion of broodmate pairs among pairs that included at least one returning nestling was 2/1394 or 1 in 694. In 197 of those 1394 pairs, both adults were returning nestlings. Therefore the proportion of returning nestlings that were involved in a broodmate pairing was 4/(1394 +197) or 1 in 397.8. Another factor to bear in mind is that the probabilities that we calculated for Ontario, based on observed broodmate pairings, were for young raised at one site in one year that subsequently bred together at a particular site in another specific year. Those probabilities are bound to be lower than the probability of detecting a broodmate pairing in any year at multiple sites. To calculate a probability equivalent to the these proportions, we would have to make calculations for each site, each year, for nestlings from each source site in each year, then add the probabilities together to get the theoretical probability (rate of detection expected per pair captured).

In conclusion, we found that inbreeding occurred more frequently than expected on our grids, but we found no clear evidence of costs to inbreeding, which suggests that selection in not acting directly on the behavior. However, we emphasize that our assessment is based on only three breeding events. If broodmate pairings are more common than expected, the conundrum becomes why they have not been observed before given the extent of research on this species. We urge other researchers to examine their data in light of these reports.

ACKNOWLEDGMENTS

The Ontario nest box sites were maintained by Long Point Bird Observatory (LPBO), Bird Studies Canada (BSC), for a long-term study of breeding performance, directed by DJTH. We thank the Ontario Ministry of Natural Resources (OMNR), the Canadian Wildlife Service, and the Canadian Department of Transport for access to the LP site; and Norfolk County, the Long Point Region Conservation Authority, and Mr. and Mrs. R.C. Stanley for use of the SL, BF and MC sites, respectively. LPBO staff assisted with logistic support. Several collaborators and numerous volunteers collected the data. LPBO/BSC funded the fieldwork expenses of volunteer assistants. This paper is a contribution of LPBO, BSC, and is OMNR Wildlife Research and Development Section Contribution No. 04-01.

In Nova Scotia, we thank the landowners of the S and L-H grids who allowed us access to their properties. We appreciate help in various forms from Colleen Barber, Anne Duncan, Richard Elliott, Keith McAloney, Adele Mullie, Emily Parks, Don Stewart, and Donna Stewart. Funding in Nova Scotia was provided by NSERC research grants to DS and ML, and an Acadia University Research and Graduate Studies Grant to DS. The manuscript was improved by the comments of Wally Rendell and anonymous reviewers.

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