

PREFERRED NEST SPACING OF AN OBLIGATE CAVITY-NESTING BIRD, THE TREE SWALLOW

ALISON MULDAL

H. LISLE GIBBS

AND

RALEIGH J. ROBERTSON

ABSTRACT.—In order to determine the preferred dispersion of a population of breeding Tree Swallows (*Tachycineta bicolor*) in Ontario, we set up an abundant supply of nest boxes with a variety of distances between them. The 72 boxes were arranged in 12 equidistantly spaced spirals. Within a spiral, the distance between boxes was much smaller than between spirals. Over five breeding seasons, we observed the order and positions in which swallows settled in the spirals. Pairs of swallows usually settled in empty spirals before settling in spirals occupied by conspecifics, but they did not avoid nesting in spirals occupied by Eastern Bluebirds (*Sialia sialis*). Swallows did not show any spacing preferences when their nearest neighbors were in different spirals, and were therefore more than 36 m away. Within spirals, however, swallows nested as far as possible from each other when their nests were less than 14 days apart. Swallow nests in the same spiral also tended to be spaced out temporally. We conclude that, over the range of distances within a spiral, Tree Swallows prefer to space their nests as far from conspecifics as possible. The observed spacing pattern probably arises from territorial behavior that is directed toward defense of a nest site from intruders.

Breeding birds disperse their nests in a variety of patterns ranging from the tightly clumped distribution of colonial species to the uniform distribution of territorial species (Lack 1968). The spatial distribution of resources such as food, nest sites, and nest materials; the intraspecific competition for these resources and for mates; and predation pressure are some of the factors determining the breeding dispersion of individuals (Crook 1965, Lack 1968, Hoogland and Sherman 1976).

In this paper, we report on an experimental approach to determine the preferred nesting dispersion of a cavity-nesting species, the Tree Swallow (*Tachycineta bicolor*). Swallows (Hirundinidae) show varying degrees of gregariousness during the breeding season. Dispersion may depend upon a particular species' nesting requirements. Some species build their own nests, while others use existing crevices in trees, rocks, and walls, or old burrows excavated by other animals.

Those species that build their own nests have some choice in the nature of their association with conspecifics, and intraspecific interactions are probably the most important determinants of their dispersion patterns (e.g., Hoogland and Sherman 1976, Snapp 1976). For example, Cave Swallows (*Hirundo fulva*) and Cliff Swallows (*H. pyrrhonota*), which build globular nests of mud pellets, breed in dense colonies, as do Bank Swallows (*Riparia ripar-*

ia; Bent 1942) and White-backed Swallows (*Cheramoeca leucosternum*), which excavate their own burrows in sand banks (Serventy and Whittell 1976). On the other hand, another burrower, the Banded Sand Martin (*Riparia cincta*), nests solitarily (McLachlan and Liv-ersidge 1965), and another mud-nest builder, the Barn Swallow (*Hirundo rustica*), nests solitarily or in loose colonies (Snapp 1976).

Those species that must nest in existing holes and cavities have distributions that are determined primarily by the availability of suitable nest sites (von Haartman 1957, Holroyd 1975). The Tree Swallow, Purple Martin (*Progne subis*), and Northern Rough-winged Swallow (*Stelgidopteryx serripennis*) are examples of obligate cavity-nesting swallows. Cavity-nesting species show considerable intraspecific variation in their nesting behavior, and may nest either solitarily or colonially, depending on the distribution of nest sites (Bent 1942). Since spacing patterns are so diverse in cavity-nesters, it is of interest to determine which, if any, nesting dispersion pattern is actually preferred. Nest spacing preferences of cavity-nesting species can be determined by providing many nest sites with different distances between them. Once the preferred spacing is known, one can begin to look for the behavioral mechanisms by which the spacing pattern is achieved, and for any effects of the spacing pattern on fitness.

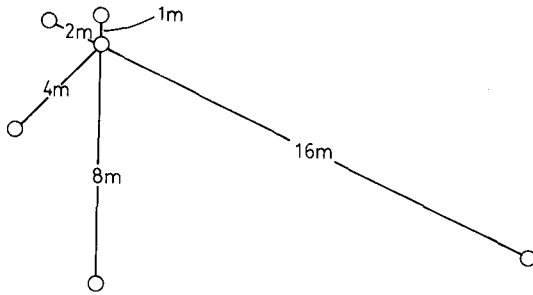


FIGURE 1. The arrangement of nest boxes in a spiral cell. The interbox distances are drawn to scale.

We sought to examine the preferred nest spacing of Tree Swallows when their choice was not constrained by the availability of nest sites. Tree Swallows were chosen because they commonly breed in Ontario and readily nest in nest boxes; thus, it was easy to manipulate the spacing of available nest sites for a sizable population of swallows. We asked the questions: (1) Do swallows tend to clump together, space out uniformly, or settle randomly in the available nest sites when they arrive at the beginning of the season? (2) Over what range of distances do swallows exhibit any spacing behavior? and, (3) Are the nesting attempts of neighboring swallows synchronized or are they temporally spaced as far apart as possible? We answered these questions by setting up a regular arrangement of nest boxes with a wide range of interbox distances, and recording the order and positions in which swallows settled during the breeding season.

METHODS

The study was done at the Queen's University Biological Station, Chaffey's Locks, Ontario, during the summers of 1977 to 1981, inclusive. The study site consisted of three adjacent hayfields of different sizes but of similar vegetation. Nest boxes mounted on 1.75-m high poles were erected in a grid of spirals, each spiral consisting of six boxes placed 1, 2, 4, 8, and 16 m from a central box (Fig. 1). This arrangement provided a variety of distances between boxes, both within a single spiral and between spirals. The entrance holes on all the boxes were oriented in the same direction so this did not affect their desirability.

One of the fields had eight spirals in a regular grid, with the central boxes of each spiral spaced 64 m from neighboring spirals. The two smaller fields had two spirals each, with the central boxes again 64 m apart (Fig. 2). The distance between boxes in neighboring spirals was in the range of 36–92 m, which greatly exceeded the distance between boxes in a single spiral (1–19 m).

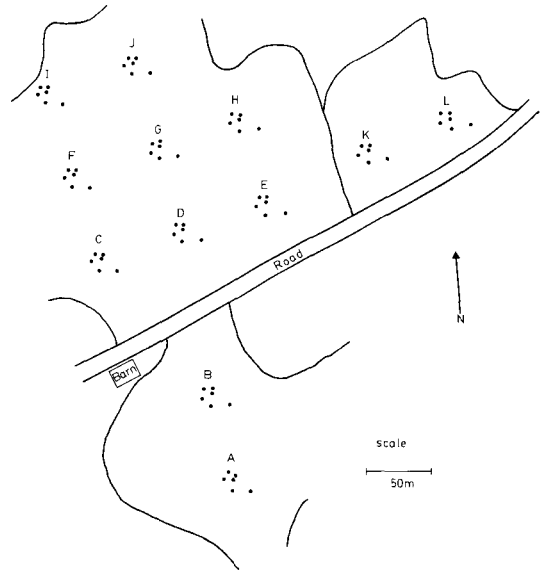


FIGURE 2. Map of the study area showing the three hayfields with the grid of spiral cells.

The nest boxes were checked early in the afternoon at 1–3-day intervals from mid-April to mid-July each year, to determine the order in which they were occupied. Since it was usually difficult to be certain of the date on which pairs settled in boxes, we used the date when the first egg was laid as an index of the settling date. From our available data, date of the first egg was highly correlated with the date when nest material first appeared in the box, which we assume to be close to the settling date ($r = 0.677$, $n = 41$, $P < 0.01$). First egg date is therefore a reasonable indicator of the order in which different pairs settled.

The spiral arrangement of nest boxes in the three fields enabled us to look at Tree Swallow settling patterns both within single spirals, where potential nearest-neighbor distances were relatively short (1–19 m), and also between different spirals, where potential nearest neighbors were relatively remote (36–92 m).

Within a spiral, there were thirteen different permutations of interbox distance. Depending on which box was chosen by the first pair of swallows settling in a spiral, a second pair nesting in an occupied spiral had a choice of five of thirteen possible nest-box distances from the first pair. The settling behavior between and within spirals was considered separately.

Non-parametric statistics were used to analyze the data (Sokal and Rohlf 1981). For the analyses of dispersion patterns, we calculated a coefficient of dispersion ($CD = \text{variance}/\text{mean}$). The difference between the calculated CD value and 1.0 indicates whether the birds were distributed uniformly ($CD < 1$), ran-

TABLE 1(a). The number of times Tree Swallows chose between empty spirals and spirals occupied by bluebirds. For each spiral category, the lefthand column gives the number chosen (O) and the righthand column gives the expected frequency (E) based on the availability of each category at each stage of the settling sequence (see text for details). 1(b). The number of times swallows chose between empty spirals and spirals occupied by conspecifics.

(a)				
Year	Empty		Bluebird	
	O	E	O	E
1977	5	5.35	1	0.65
1978	11	8.90	0	2.10
1979	4	5.62	3	1.38
1980	9	7.69	2	3.31
1981	6	6.75	4	3.25
Total	35	34.31	10	10.69

(b)				
Year	Empty		Swallow	
	O	E	O	E
1977	10	5.44	2	6.56
1978	10	5.45	1	5.55
1979	7	4.14	1	3.86
1980	8	4.00	0	4.00
1981	6	3.66	1	3.34
Total	41	22.69	5	23.31

domly ($CD = 1$), or in a clumped fashion ($CD > 1$). Data were tested against a positive binomial (uniform) distribution using a Chi-squared test for goodness-of-fit (Elliot 1973).

RESULTS

SETTLING PATTERN BETWEEN SPIRALS

The occupancy rate of all of the nest boxes was relatively low each year (1977–35%; 1978–24%; 1979–24%; 1980–22%; 1981–29%), suggesting that nest sites were plentiful for this population of swallows.

To test whether Tree Swallows preferred particular spirals in the grid, we used a Kruskal-Wallis ANOVA test on the annual order of settling in the twelve spirals. Since swallows did not tend to choose spirals in any particular order each year ($H = 5.58$, $P = 0.899$), we concluded that all spirals in the grid were equally attractive during the settling sequence.

If the swallows preferred to clump their nests, we would have expected to find two or more pairs settling in the same spiral, even when empty spirals were still available. If the birds spaced themselves perfectly uniformly, each of the twelve spirals should have been occupied by a single pair of swallows before any of them was occupied by a second pair. By examining the sequence of settling in the spirals, we tested the hypothesis that swallows chose randomly among the available boxes.

At our study site, several pairs of Eastern Bluebirds (*Sialia sialis*) became established in

nest boxes before the Tree Swallows arrived in the spring (1977, 1978—one pair; 1979, 1980—three pairs; 1981—four pairs). Bluebirds aggressively compete with Tree Swallows for nest sites when these are in short supply (Kuerzi 1941). Although boxes were abundant, (on average, only 3% were already occupied by bluebirds when the swallows arrived in the spring), it was important to ascertain first whether swallows avoided nesting in the same spirals as bluebirds, or whether they “ignored” bluebirds.

As settling progressed, the number of empty spirals and spirals containing swallows changed. Each time a new pair (or pairs) settled in the spirals, we computed *a posteriori* the number of spirals available that were either empty or occupied by Tree Swallows or bluebirds, and the number of empty and occupied spirals that were actually chosen by swallows. The expected number of times that empty or occupied spirals would be chosen randomly was calculated by summing the probability of each category of spiral (i.e., empty, occupied by swallows, or by bluebirds) that was chosen at each stage in the settling sequence. Deviations of the swallows' observed choices from the expected values were then compared to a standard normal distribution using the Z statistic (Sokal and Rohlf 1981). Since the probability of swallows choosing spirals in each category changed continually as more swallows settled, Z was calculated using the formula:

$$Z = \frac{\text{observed-expected choice}}{\sqrt{\sum \text{product of probabilities for each spiral category}}}$$

which takes into account the changing variance.

When swallows had a choice between empty spirals and spirals occupied by bluebirds, 10 of 45 (22%) settled in spirals occupied by bluebirds (Table 1a). This result is not significantly different from a random settling pattern when compared with empty spirals ($Z = 0.25$, $P = 0.40$). Although there were more than three times as many spirals available that were occupied by other swallows than by bluebirds, only five of 46 (11%) swallows chose spirals occupied by conspecifics (Table 1b). This differed markedly from a random settling pattern ($Z = 6.20$, $P \ll 0.001$). Therefore, Tree Swallows spaced themselves with respect to conspecifics until all the spirals were occupied by a single pair of swallows, but they settled randomly in spirals occupied by bluebirds.

TABLE 2. Annual frequency distributions of the maximum number of nest boxes occupied concurrently per spiral.

Year	Frequency of concurrently occupied boxes per spiral							Mean	CD	χ^2*	P
	0	1	2	3	4	5	6				
1977	0	2	8	2	0	0	0	2.00	0.18	2.00	<0.005
1978	0	10	2	0	0	0	0	1.67	0.13	1.00	<0.005
1979	0	9	2	1	0	0	0	1.33	0.32	3.50	<0.025
1980	0	9	3	0	0	0	0	1.25	0.16	1.80	<0.005
1981	0	6	4	2	0	0	0	1.67	0.36	4.00	<0.05

* Relative to a positive binomial distribution.

The coefficient of dispersion for concurrently nesting swallows was significantly less than 1.0 in each year, which also indicates that the final distribution of concurrently nesting pairs among spirals was uniform (Table 2).

To see whether the swallows preferred to space themselves at relatively great distances, we tested the hypothesis that, during the settling sequence in the grid, birds would choose the empty spiral closest to a spiral occupied by a conspecific at a random-level frequency. Hereafter, only spirals occupied by Tree Swallows are referred to as "occupied." Since the central boxes of each spiral in a particular field were evenly spaced in a grid at 64-m intervals, and distances between boxes within spirals were much smaller than distances between spirals (1–19 m vs. 36–92 m, respectively), a spiral was defined as "close" to an occupied site if it was an immediate neighbor to an occupied spiral, and "far away" if it was two or more spirals from the nearest occupied site. Spirals in different fields were considered far from one another. From the first egg dates, we determined *a posteriori* how many spirals close to and far from occupied spirals were available each time a new pair, or pairs, settled, and then compared this with the number of close and far sites actually chosen by Tree Swallows. This procedure was done for each step in the settling sequence where swallows had a choice between "close" and "far" sites. The expected number

of times close and far spirals would be randomly chosen was calculated by the method described earlier. The birds' observed choices were then compared with these expected values.

The results suggest a random settling pattern (Table 3). Tree Swallows neither preferred nor avoided settling in a spiral that was close to another occupied spiral ($Z = 0.75$, $P = 0.23$) over distances in the range of 36–92 m.

SETTLING PATTERN WITHIN SPIRALS

To see whether swallows tended to space their nests away from relatively close neighbors, we looked at which boxes were chosen by the second pairs to settle in occupied spirals. We listed the nest-box distances available to the second pair, given the position in which the first pair settled, and then compared this with the distance actually chosen by the second pair.

The results in Table 4 show that the second pairs of swallows to nest in spirals significantly more often chose the box farthest from the original occupants than any other box in the spiral ($\chi^2 = 22.10$, $P < 0.001$). In the three cases where the closest box was chosen, it was at distances of 14, 14, and 16 m, respectively. Tree Swallows chose proportionately more of the available boxes at greater distances from the resident pair (Fig. 3). Within spirals, therefore, Tree Swallows tended to space their nests away from their nearest neighbors.

TABLE 3. Frequency with which Tree Swallows chose spirals "close" to, and "far" from, occupied spirals. Left-hand columns give number of close and far spirals actually chosen, righthand columns give expected choices based on the availability of close and far spirals at each step in the settling sequence (see text for details).

Year	Close		Far	
	O	E	O	E
1977	2	3.37	4	2.63
1978	3	3.31	3	2.69
1979	4	4.72	3	2.28
1980	4	3.58	3	3.42
1981	4	3.90	2	2.10
Total	17	18.88	15	13.12

TABLE 4. The number of times second pairs of Tree Swallows that settled in the spirals chose the box closest to, or farthest from, the box occupied by the resident pair, or any other box in the spiral. For each category of box, the lefthand columns give the observed (O) and the righthand columns give the expected (E) frequencies.

Year	Number of times box chosen					
	Closest		Farthest		Other	
	O	E	O	E	O	E
1977	1	1.8	5	1.8	3	5.4
1978	0	1.0	2	1.0	3	3.0
1979	1	0.4	1	0.4	0	1.2
1980	0	0.6	2	0.6	1	1.8
1981	1	1.0	4	1.0	0	3.0
Total	3	4.8	14	4.8	7	14.4

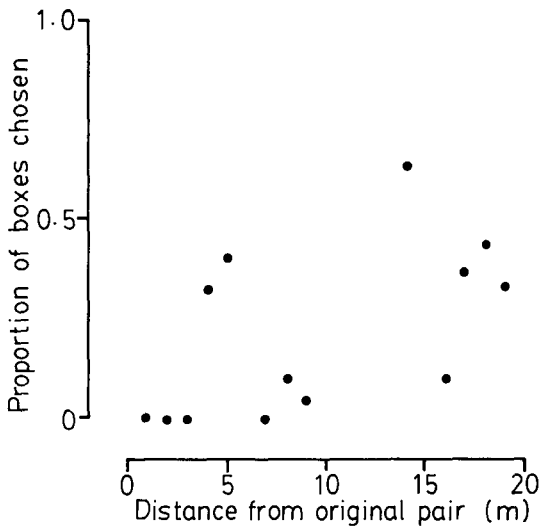


FIGURE 3. The proportion of available boxes chosen by second pairs of swallows nesting in spirals, in relation to the distance of the chosen boxes from the original occupants of the spirals. Spearman's rank correlation $r = 0.637$, $P < 0.02$.

TEMPORAL SPACING

The first swallows to nest in the spirals each year were highly synchronized with one another, with 68% of the birds (± 1 SD from the mean) laying their first eggs within three days of the mean for the population (data from five years combined). The second pairs to nest in occupied spirals, however, laid their first eggs, on average, 13 days later than the first pairs. Nests within spirals therefore tended to be temporally spaced out from one another.

Within a spiral, the closer together the nests were in time, the farther the second pair's nest was from the first (Fig. 4). From inspection of the figure, it seemed that behavior might switch as the interval between first and second nests increased, from choosing only boxes farthest from the nearest neighbor, to choosing boxes randomly. Dividing the data in half, we found that swallows that started nests less than 14 days after the first pair in the spiral were significantly more likely to choose the box farthest from the first pair than any other box in the spiral ($\chi^2 = 22.72$, $P < 0.001$), while the choice of nests initiated more than 14 days after the first pair had settled was not significantly different from random ($\chi^2 = 3.56$, $P > 0.1$).

DISCUSSION

Although Tree Swallows have been reported to nest colonially (Whittle 1926, Sheppard 1977), those in this Ontario population did not choose to nest close together when there were abundant suitable nest sites. Our results demonstrate both spatial and temporal spacing of

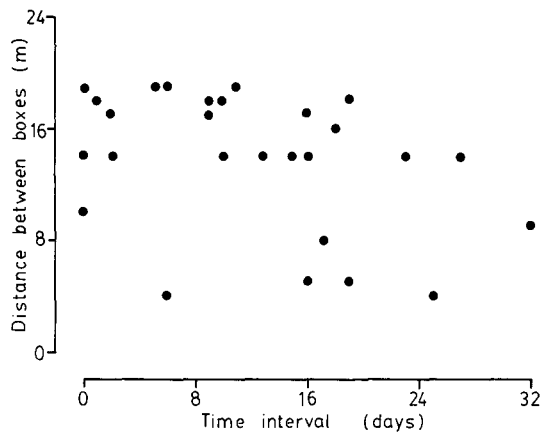


FIGURE 4. The relationship of the time interval between two pairs of swallows nesting in the same spiral to the distance between the two nests. Data from five years for 27 spirals occupied concurrently by two pairs. Spearman's rank correlation $r = 0.375$, $P < 0.05$.

nests at close distances. In studies at other sites, Tree Swallows nested much closer than we observed in our study. They nested in boxes 2–4 m apart in Massachusetts (Whittle 1926), 15.2 m apart in Connecticut (Kuerzi 1941), and 10 m apart in New York (Sheppard 1977). Harris (1979), in New Brunswick, noted four pairs nesting in a single spiral similar to ours and also documented one successful nesting in a pair of boxes only 1 m apart. The temporal separation of the nests, however, was not mentioned in any of these studies; it is therefore possible that although the nests were close together in distance, they may have been widely separated in time.

The very high occupancy rates documented in some of these earlier studies suggest that population pressure may have resulted in closer spacing of nests. The occupancy rate for our population was relatively low (on average, only 45% of the boxes 4 m or more apart were occupied). With high occupancy rates, it is likely that the availability of nest sites determines the observed spacing pattern. We can be fairly confident, however, that nest sites were not limiting in our study site, and that we observed the preferred spacing pattern of Tree Swallows in the spirals.

The spacing pattern we found may have arisen either from avoidance of occupied boxes by arriving swallows, or from aggression by resident swallows, preventing others from settling close by. It is difficult to distinguish between these two possibilities from our data. The spacing pattern at the beginning of the breeding season, when arriving swallows tended to settle in empty spirals while these were available, may have arisen as a result of avoidance behavior by the arriving swallows. It is

likely, however, that the spacing pattern later in the season, when second pairs settled in spirals as far as possible from the resident pair, resulted from the aggressive behavior of the resident pair.

That Tree Swallows are aggressive towards conspecifics has been reported by several authors (Kuerzi 1941; Harris 1979; Leffelaar and Robertson 1985). In an experiment using stuffed models of Tree Swallows, Robertson and Gibbs (1982) showed that resident Tree Swallows were aggressive at distances of up to 8 m from their nest box, and that aggression was centered around the box. They concluded from the model tests that one function of intraspecific aggression was the territorial defense of a nest site from usurpation by conspecifics, and that Tree Swallows defended symmetrical territories of 6–8 m radius around their nest sites. These results suggest that aggression is an important behavioral mechanism that determines nest spacing patterns, although avoidance may be operating as well.

When Tree Swallows first settled in the grid, each spiral of six boxes was defended by a single pair, and an average of 13 days elapsed before a second pair settled into any of the spirals. We can offer two possible explanations for this temporal spacing. (1) It may be a function of the pattern of arrival of birds into the area. Second-year brown female Tree Swallows are known to arrive in their breeding areas 2–3 weeks later than blue-green adults (Kuerzi 1941). At our study site, however, only four or five second-year females settled in the grid each year; therefore, a late wave of settling second-year females can only partially account for the observed 13-day temporal spacing between the first and second pairs nesting in the spirals. (2) Resident swallows might actively prevent other pairs from settling in the spiral for approximately 13 days, but then might relax their defense as they become involved in incubation and the feeding of nestlings, so that the defended area becomes smaller with time. Behavioral observations of breeding swallows indicate that aggression decreases as the breeding season progresses. Gibbs (1980) found that Tree Swallows were most aggressive towards conspecifics when nest sites were being chosen, before nest-building began. A pair's aggressive response dropped off during the nest-building period, and declined further as the breeding cycle progressed. Stutchbury (1984) also found that aggressive responses of breeding Tree Swallows towards models of conspecifics decreased as the nesting cycle progressed. Aggression between Eastern Bluebirds similarly declines during the breeding season (Gowaty 1981). A decrease in territory size during the

breeding cycle has also been reported for Purple Martins, which usually defend more than one room of a martin house at the start of the breeding season, but defend fewer rooms as the breeding season progresses (Brown 1979).

We can offer several alternative hypotheses for the function of territoriality in Tree Swallows: (1) Tree Swallows might prevent other individuals from nesting close to them because there is some fitness-related disadvantage to nesting at high densities; for example, increased competition for food or other necessary resources, higher risk of cuckoldry, predation, or parasitism (e.g., Davies 1978). (2) Tree Swallows might defend territories, including boxes additional to that required for nesting, either in order to (a) enable males to be polygamous (Brown 1979), or (b) prevent other birds in the population from breeding, thus increasing the resident's relative genetic contribution to future generations (Harris 1979). (3) Tree Swallows might defend territories as the most efficient means of defending a nest site from intruders (Hinde 1956).

Tree Swallows do not defend feeding territories, since they feed almost entirely on highly mobile, aerial insects, a resource which would be difficult to defend (Kuerzi 1941, Sheppard 1977). Thus, we would not expect that nest spacing would be a factor influencing fitness through competition for food. Although little predation existed in our population, there may have been a density-related effect on fitness of blowfly larval (*Protocalliphora* sp.) parasitism of nestlings, which was sometimes severe.

Brown (1979) suggested that male Purple Martins defended more than one room of a martin house early in the breeding season in order to have the potential to mate polygynously. Five percent of males in his population were polygynous. Quinney (1983) found that 5% of male Tree Swallows at a site with relatively abundant food were polygynous. Polygyny in our population was rare, however, and since in most reported cases polygyny involved two females nesting in the same box (Quinney 1983; this study), it is unlikely that males in our population defended extra boxes to obtain additional mates.

Harris (1979) suggested that Tree Swallows defended territories containing extra boxes in order to prevent other individuals in the population from breeding. This is the "superterritory" hypothesis of Verner (1977). Robertson and Gibbs (1982) showed in their study site, however, that territorial defense was not oriented towards additional nest boxes and, furthermore, relative territory size was the same for solitary-nesting birds as for those that had the potential to defend extra boxes.

We suggest instead that the most likely ultimate reasons for Tree Swallow territoriality are the defense of the nest site against competitors, which may be achieved most effectively by defending a certain minimum space around the nest site (Hinde 1956), and the avoidance of cuckoldry by males. The reported decline in aggression during the breeding season (Gibbs 1980, Stutchbury 1984) supports the hypothesis that aggression between females is directed towards protection of the nest site from intruders, rather than toward defense of food or against predators (Gowaty 1981). Since male Tree Swallows do not guard their mates during their fertile periods (Leffelaar and Robertson 1984), aggression between males near the nest box may serve to reduce the risk of cuckoldry. The decline in aggression of males during the breeding season is consistent with protection of paternity and also with defense of the nest site against conspecific intruders. Both members of the pair also vigorously defend their nest site from other cavity-nesting species, such as bluebirds, Purple Martins, House Sparrows (*Passer domesticus*), and House Wrens (*Troglodytes aedon*; Kuerzi 1941).

Defense of an area around the nest site has been reported for other cavity-nesting species. Pied Flycatchers (*Ficedula hypoleuca*) defend an area of radius 0–10 m around the nest site, and the only function of this defense is to protect ownership of the nest site (von Haartman 1956). Brown-chested Martins (*Phaeoprogne tapera*) in Venezuela fight at the entrances to nest holes when more than one nest is present in the vicinity (Turner 1984). They are territorial, nesting singly or in small groups in dead trees and in holes in bridges. In Panama, Mangrove Swallows (*Tachycineta albilinea*) and Gray-breasted Martins (*Progne chalybea*) disperse in nest boxes, with only single pairs occupying groups of boxes (Dyrce 1984). The distance between neighboring pairs is always several hundred meters. Mangrove Swallow territories, unlike those of Tree Swallows, are also used as foraging areas, there being only a small area of overlap of feeding activity between neighboring territories.

Our study demonstrates that Tree Swallows, when given the choice, space their nests both spatially and temporally. This seems to be related to defense of nest sites, which are often limiting for obligate cavity-nesters (von Haartman 1957, Holroyd 1975).

ACKNOWLEDGMENTS

We are grateful for the field assistance of Shelagh Hurley Mathers in 1980 and Lesley Cameron in 1981. We thank Malcolm Griffin and Pete Blancher for help with statistics,

and Philip Stoddard, Edward Burtt and members of the "Bird Lab" for helpful comments on the manuscript. Field facilities and accommodation were provided by Queen's University Biological Station. This study was funded by a grant to RJR from the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

- BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179.
- BROWN, C. R. 1979. Territoriality in the Purple Martin. Wilson Bull. 91:583–591.
- CROOK, J. H. 1965. The adaptive significance of avian social organization. Symp. Zool. Soc. Lond. 14:181–218.
- DAVIES, N. B. 1978. Ecological questions about territorial behaviour, pp. 317–350. In J. R. Krebs and N. B. Davies [eds.], Behavioural ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford.
- DYRCZ, A. 1984. Breeding biology of the Mangrove Swallow (*Tachycineta albilinea*) and the Gray-breasted Martin (*Progne chalybea*) at Barro Colorado Island, Panama. Ibis 126:59–66.
- ELLIOT, J. M. 1973. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. 25.
- GIBBS, H. L. 1980. Spacing behavior of nesting Tree Swallows (*Iridoprocne bicolor*): the dispersion pattern and its determinants. B.Sc. thesis, Queen's University, Kingston, Ontario.
- GOWATY, P. A. 1981. Aggression of breeding Eastern Bluebirds (*Sialia sialis*) toward their mates and models of intra- and interspecific intruders. Anim. Behav. 29:1013–1027.
- HARRIS, R. W. 1979. Aggression, superterritories and reproductive success in Tree Swallows. Can. J. Zool. 57:2072–2078.
- HINDE, R. A. 1956. The biological significance of territoriality in birds. Ibis 98:340–369.
- HOLROYD, G. L. 1975. Nest site availability as a factor limiting population size of swallows. Can. Field-Nat. 89:60–64.
- HOOGLAND, J. L., AND P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecol. Monogr. 46:33–58.
- KUERZI, R. G. 1941. Life history studies of the Tree Swallow. Proc. Linn. Soc. N. Y. 52–53:1–52.
- LACK, D. 1968. Ecological adaptation for breeding in birds. Methuen and Co., London.
- LEFFELAAR, D., AND R. J. ROBERTSON. 1984. Do male Tree Swallows guard their mates? Behav. Ecol. Sociobiol. 16:73–79.
- LEFFELAAR, D., AND R. J. ROBERTSON. 1985. Nest usurpation and female competition for breeding opportunities in the Tree Swallow. Wilson Bull. 97:221–224.
- MCLACHLAN, G. R., AND R. LIVERSIDGE. 1965. Roberts birds of South Africa. Trustees of the South African Bird Book Fund.
- QUINNEY, T. E. 1983. Tree Swallows cross a polygyny threshold. Auk 100:750–754.
- ROBERTSON, R. J., AND H. L. GIBBS. 1982. Superterritoriality in Tree Swallows: a reexamination. Condor 84:313–316.
- SERVENTY, D. L., AND H. M. WHITTILL. 1976. Birds of Western Australia. Univ. of Western Australia Press, Perth.
- SHEPPARD, C. D. 1977. Breeding in the Tree Swallow (*Iridoprocne bicolor*) and its implications for the evolution of coloniality. Ph.D. diss., Cornell Univ., Ithaca, NY.

- SNAPP, B. D. 1976. Colonial breeding in the Barn Swallow (*Hirundo rustica*) and its adaptive significance. *Condor* 78:471-480.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry. The principles and practice of statistics in biological research.* W. H. Freeman and Co., San Francisco.
- STUTCHBURY, B. J. 1984. The adaptive significance of delayed plumage maturation in female Tree Swallows (*Tachycineta bicolor*). B.Sc. thesis, Queen's Univ., Kingston, Ontario.
- TURNER, A. K. 1984. Nesting and feeding habits of Brown-chested Martins in relation to weather conditions. *Condor* 86:30-35.
- VERNER, J. 1977. On the adaptive significance of territoriality. *Am. Nat.* 111:769-775.
- VON HAARTMAN, L. 1956. Territory in the Pied Flycatcher, *Muscicapa hypoleuca*. *Ibis* 98:460-475.
- VON HAARTMAN, L. 1957. Adaptation in hole-nesting birds. *Evolution* 11:339-347.
- WHITTLE, C. L. 1926. Notes on the nesting habits of Tree Swallows. *Auk* 43:247-248.
- Biology Department, Queen's University, Kingston, Ontario K7L 3N6. Address of second author: Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109-1048. Received 19 July 1984. Final acceptance 23 February 1985.*