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SUPERTERRITORIALITY IN TREE SWALLOWS: A REEXAMINATION

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ABSTRACT.—Field experiments were conducted on a population of nesting Tree Swallows (*Iridoprocne bicolor*) to assess whether the evolved function of territoriality is to prevent breeding by conspecifics (superterritoriality). The size and orientation of territories were estimated by the response of birds to a conspecific model. There was no difference in territory size between birds that had the potential to defend surplus boxes and those that did not. Similarly, territorial defense was not oriented more toward the vicinity of surplus boxes than in other directions. These results indicate that territorial behavior has not evolved due to a relative increase in fitness that may be gained by preventing conspecifics from breeding.

Verner (1977) proposed that an important function of avian territorial behavior is limitation of successful reproduction by conspecifics. Although the idea has been criticized as being theoretically unsound (Davies 1978, Colgan 1979, Getty 1979, Parker and Knowlton 1980), Harris (1979) claimed to have demonstrated the existence of "superterritories" in a population of breeding Tree Swallows (*Iridoprocne bicolor*). He observed defense of more than one nestbox by pairs of birds and concluded that this represented superterritorial behavior because 1) such boxes represented an additional resource not necessary for successful reproduction by the resident pair and 2) potential breeders were prevented from using the defended boxes, thereby increasing the relative proportion of the resident pair's genetic contribution to future generations. Harris' (1979) argument, therefore, implies that an important force behind the evolution of territoriality in this species is the prevention of nesting by other potential breeders.

However, as Harris (1979) suggested, an alternate explanation for the existence of multibox territories is possible. Swallows could simply be defending a certain minimum space around their nest site regardless of whether or not additional nestboxes were included within this space. Hinde (1956) suggested that such behavior would allow individuals of certain species to defend single nest sites more effectively against competitors. If this were the case, the evolutionary function of such behavior would not be defense of excess resources, but defense of an essential resource. The evolutionary background and implications of these two functions of territoriality, while not mutually exclusive, are very different and must be distinguished.

The purpose of this paper is to present data showing that Tree Swallow territorial defense, and hence relative territory size, is not influenced by the presence or absence of empty nestboxes. This indicates that the value of holding a territory is not directly related to the reduction of breeding by conspecifics. We therefore argue that the "superterritories" found by Harris (1979) do not represent superterritories in the evolutionary sense described by Verner (1977).

METHODS

STUDY AREA

This study was conducted from 26 April to 15 May 1980 on Tree Swallows breeding in nestboxes at Queen's University Biological Station, Chaffey's Locks, 50 km north of Kingston, Ontario. These dates correspond to the pre-egg-laying period of the reproductive cycle, when aggressive defense of nest sites is most intense. Observations were made on birds breeding in nestbox grids situated in two hayfields of different size but similar vegetational composition. Within grids, boxes were arranged in two types of spatial patterns: 1) boxes located in roughly evenly spaced rows approximately 25 m apart and 2) boxes situated in groups of six, with sites arranged in a spiral pattern such that boxes were 1 m, 2 m, 4 m, 8 m, and 16 m away from the central box. Boxes were arranged in this manner in 1977 for use in an experimental study of the spacing behavior of this species. However, the variable spacing of the boxes also provided an opportunity to test the superterritory hypothesis. Harris (1979) used a similar pattern in his study.

TERRITORY SIZES

In order to examine the sensitivity of territorial defense, and hence our relative estimates of territory size, to the presence of surplus nest sites, we selected 13 occupied nestboxes and divided them into two categories, clumped boxes (CB) and solitary boxes (SB). CB represented potential superterritories since empty boxes fell within a distance less than or equal to the maximum distance at which Harris (1979) reported empty boxes were defended, while SB, due to a lack of nearby boxes, did not. Clumped boxes ($n = 6$) had at least one empty box within 3.5 m of the occupied box (in five out of the six boxes included within this category, empty boxes were within 1.5 m of the occupied box). Solitary boxes ($n = 7$) had no empty boxes present within 14 m of the occupied box. In all cases, CB were either the central box in a spiral or one of the boxes 1, 2, or 4 m from the central box in a spiral, while six out of the seven SB were situated in linear grids. The other SB used was one that was 16 m away from the central box in a spiral.

The strength of territorial defense by birds in these two situations was used to estimate relative territory sizes. We measured territorial defense by recording the number of dives made by a resident pair toward a stuffed male Tree Swallow model attached to a 1.5-m pole and placed at distances of 6, 8, and 10 m from the occupied box. The response of the pair over a three-minute period was recorded by an observer crouching approximately 30 m away from the box. Model presentation was randomized both with respect to distance, compass direction (N, S, E, W) relative to the tested box, and date throughout the study period. Two to five tests were conducted on each pair at each distance, with four or five tests carried out in most cases. On any given day, a maximum of two tests was conducted on an individual, with at least one hour between tests. To determine if this rate of exposure caused any habituation or carry-over effects in the bird's behavior, we selected nine pairs of birds and tested them twice at 6 m with one hour between model presentations. Using number of dives as a measure of a pair's aggressiveness, response levels did not differ significantly between the first and second trials (Wilcoxon signed-ranks test, $T = 6$, $df = 9$, $P > 0.05$) indicating that no exposure effect was present.

We emphasize that the model tests allow only a relative estimate of territory size to be made. The birds were probably far more responsive to live intruders than to a stuffed model (for an example of this phenomenon, see Shalter 1978). We assumed that a consistent relationship existed between relative and actual territory size in both CB and SB situations.

Initial examination of the response data showed that they were not normally distributed. Therefore non-parametric statistics, as outlined in Conover (1980), were used in all analyses.

RESULTS

At each distance tested, the median number of dives at the Tree Swallow model by pairs in clumped boxes was not significantly different from that of pairs in solitary boxes (Fig. 1). Birds that did not have the potential to defend extra boxes appeared to respond just as vigorously to an intruder as those that did.

In comparing response levels versus distance, most birds in both SB and CB situations responded to the model in some way at 6 m (CB, five out of six birds; SB, six out of seven birds) while very few individuals responded at 8 m (CB, two out of six birds; SB, one out of seven birds) or at 10 m (CB, two out of six birds; SB, two out of seven birds). Therefore, an estimate of the radius of a territory based on responses to a model would be between 6 m and 8 m in both SB and CB situations. These results suggest that territories of nesting Tree Swallows in the population studied have the same relative size, whether or not surplus boxes are present.

If Tree Swallows defend superterritories, another prediction is that territory shape should be closely related to the distribution of empty nest boxes. That is, birds should respond most intensely to the model when it is placed close to empty boxes. All occupied CB boxes had one compass direction (south) in which the model was substantially closer to the empty boxes present (mean distance of model to empty box, 2.25 m + 0.61 SD) than for any other direction (mean distance of model to empty box, 4.56 m + 1.16 SD). To test the hypothesis that birds should respond more vigorously to the model in this direction, we compared the distribution functions for the number of dives over all trials at 6 m for each compass direction using a Kruskal-Wallis test for K independent samples. The distributions were not found to be significantly different from one another ($T = 5.7$, $P > 0.05$). This result supports the idea that birds were defending the space around their nest sites in all directions, and not preferentially the extra boxes.

DISCUSSION

Our study shows that 1) relative territory size is the same in solitary-nesting Tree Swallows and in those that have the potential to defend excess resources in the form of nestboxes and

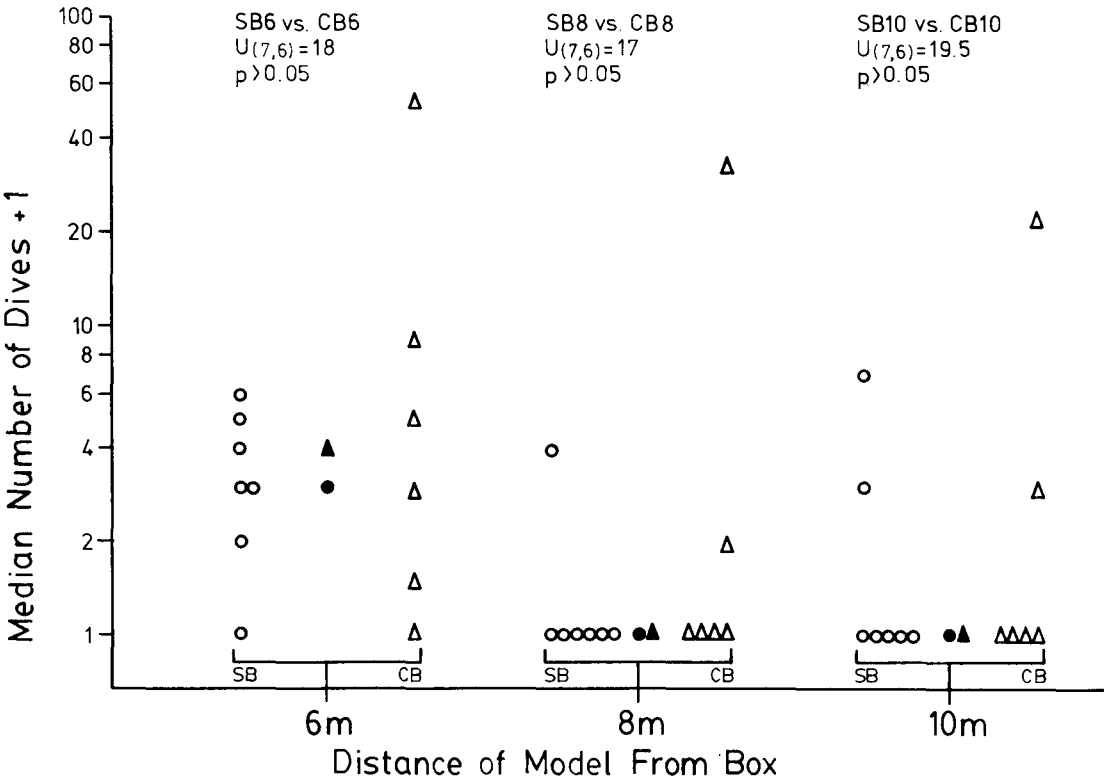

FIGURE 1. The relationship between response levels of resident birds and the distance from the nestbox at which the model was presented in Clumped Box (CB) and Solitary Box (SB) situations. Each open symbol represents the median value for 2 to 5 tests performed on a given pair of birds. Overall median values are shown as closed symbols. All CB values greater than 30 are from the same pair of birds. Median number of dives + 1 was used to enable the use of a semilog graph. U is the Mann-Whitney statistic.

2) individuals do not appear to selectively orient their territorial defense in relation to the location of the surplus nest sites, but rather defend circular areas around their boxes. Clearly, these results indicate that territorial behavior in Tree Swallows has not evolved due to the relative increase in fitness gained by preventing conspecifics from breeding.

We emphasize that we do not dispute Harris' (1979) claim that the swallows he studied did defend superterritories in an operational sense. In fact, some birds in our study area have territories which encompass more than one nest box (Gibbs and Robertson, unpubl.). Our objection is to Harris' (1979) contention that the evolutionary function of territoriality in this species is to limit reproduction by conspecifics.

Another argument against the presence of superterritorial behavior is that it can evolve only under a very restricted set of ecological conditions. Population sizes must be small, cost of defending the excess resources must be low, and gene flow between populations limited (Rothstein 1979). Although the first two conditions are probably met by Tree Swallows (Harris 1979), genetic exchange between populations does not seem to be restricted. Estimates of gene flow are relatively simple to obtain for this species, since both adults and young are easily captured and banded. Several studies document the annual rates of return by banded Tree Swallows to nesting areas. Perhaps the most detailed is the one by Chapman (1955). Analysis of fourteen years of data suggested that in his study grid, the population consisted, on average, of 44% birds previously banded as adults or nestlings and 56% unbanded birds. The latter figure compares favorably with values obtained for shorter and less complete studies [Low (1933) 59%; Kuerzi (1941) 63%; this study, 55%]. These values indicate that gene flow between Tree Swallow populations is high. As a result, the swamping effect of gene flow would prevent superterritoriality from ever being established in a population due to its positive frequency dependence (Rothstein 1979).

Given these arguments, we suggest that the defense of more than one nestbox observed by

Harris (1979) is an artifact of the densely clumped distribution of boxes in his study grid. Boxes were so closely spaced together that defense of a single site entailed inclusion of other boxes in a territory.

Two alternate hypotheses for the function of territorial behavior in this species are that 1) Tree Swallows prevent other individuals from nesting close to them because this would result in either competition for food or some other fitness-related disadvantage, 2) birds that are territorial may reduce the probability of their nest site being usurped by other pairs. Support for the latter hypothesis comes from observations that other hole-nesting species possess territories with no function other than defense of a nest site. For example, resident Pied Flycatchers (*Ficedula hypoleuca*) strongly defend their nestbox against conspecifics at distances of up to 10 m (von Haartmann 1956). Tests of the first hypothesis, focusing on the relationship between nesting density, competition for food, competition for feathers for nest lining, and risk of cuckoldry are part of our continuing studies on Tree Swallows.

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