

## DEFENSE OF EXTRA NEST-SITES BY A CAVITY NESTING BIRD, THE TREE SWALLOW *Tachycineta bicolor*

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**ABSTRACT** We use data from field experiments and observations of Tree Swallows *Tachycineta bicolor* defending single and extra nest-sites at nest-box and cavity populations to determine the function of extra nest-site defense behaviour. About 50% of pairs travelled up to 56 m to defend neighbouring nest-sites for a month or longer. Both sexes defended extra nest-sites. Males spent more time than females at extra nest-sites, especially during later stages of the breeding cycle. In Experiment 1, 60% of extra nest-sites erected beside occupied nestboxes were defended by a neighbouring settled pair. In Experiment 2, males, and perhaps females, preferred to settle on territories with two nest-sites versus those with one. There were no age differences for either sex when comparing birds which defended extra nest-sites with those that did not. Physical characteristics of males were not different between defense types, but females that defended extra nest-sites had longer wings than those that defended one nest-site. Although they may be beneficial in cases where a nest-site is destroyed by a predator, extra nest-sites were usually not essential for re-nesting. Residents were evicted from territories with extra nest-sites as often as those with only one nest-site. Polygyny was not observed in the natural populations, but one quarter of males with extra nest-sites in the nestbox populations attracted a second female. Our data suggest that male Tree Swallows exhibit resource defense polygyny, and females probably defend extra nest-sites to prevent or delay settlement by other females.

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### INTRODUCTION

An important function of territoriality is to defend resources essential for breeding (Brown 1964). For secondary cavity-nesting birds suitable nest-sites are often a limiting resource (Von Haartman 1957, 1969; Holroyd 1975), so territorial behaviour functions to acquire and defend cavities. In Tree Swallows *Tachycineta bicolor* limited availability of cavities results in considerable competition. Males and females arrive at breeding sites in very early spring and begin defending one or more cavities (Robertson *et al.* 1992). The area immediately surrounding the cavity or cavities is defended against intruders as a territory. Territorial defense involves one or both members of a pair spending extensive periods of time perched on or near the nest site, and intercepting and chasing in-

truders that encroach and persist for more than a few seconds in the vicinity of the nest-site. Females are often more vigilant and aggressive than males, especially when repelling female intruders (Stutchbury & Robertson 1987d). When birds are off territory they are generally foraging at distances from 50 to several hundred metres from the territory. While within sight of the territory, they respond to intruders; otherwise intruders are evicted upon the return of the residents to the territory. Those birds that do not get nest-sites become floaters (Stutchbury & Robertson 1985), intrude on residents' territories (Lombardo 1986b) and will displace or quickly replace residents (Stutchbury & Robertson 1987a). Competition for nest-sites can escalate to fights causing injury and death (Leffelaar & Robertson 1985, Lombardo 1986a, Robertson *et al.* 1986). Despite this severe

competition, we have observed that many pairs of Tree Swallows aggressively defend more than one nest-site. We call this behaviour extra nest-site defense, which is distinct from polyterritoriality (cf. Alatalo & Lundberg 1984, Slagsvold & Lifjeld 1988) because the nest-sites that are defended are on a contiguous territory.

We hypothesize that defense of extra nest-sites may serve several different functions for males and females. (1) Males may become polygynous by attracting a secondary female to the extra nest-site (e.g., Johnson & Kermott 1991, Stutchbury 1991). Polygyny occurs consistently, albeit in low frequency, in populations of Tree Swallows (Dunn & Hannon 1991, Dunn & Robertson 1992). If an extra nest-site is necessary for males to attract a second female then polygyny should occur more often on territories where males defend more than one nest-site compared to territories where males defend a single nest-site. Females, in turn, may defend extra nest-sites to prevent settlement by secondary females, and thereby eliminate any chance of sharing male assistance (cf. Slagsvold & Lifjeld 1994). (2) Extra nest-sites may improve mate retention for males because females could reneest in alternate cavities after the failure of an earlier breeding attempt (Robertson *et al.* 1986, Slagsvold & Lifjeld 1986). Tree Swallows raise one brood annually, but will reneest if a breeding attempt fails early in the breeding season (Robertson *et al.* 1992). Therefore, after the failure of a breeding attempt, females could use extra nest-sites for reneesting, and males defending extra nest-sites should be more likely to retain their original mate than males with one nest-site. (3) Defense of extra nest-sites by males may act as a cue to females concerning male quality, and therefore function in mate choice (Slagsvold & Lifjeld 1986). Assuming that defense of larger territories by Tree Swallows is energetically costly and dangerous, males that manage to acquire and defend one or more extra nest-sites should be of higher quality, i.e. physically larger and/or more experienced, than males defending one nest-site and females should prefer to settle and mate with higher quality males. (4)

Extra cavities could serve as territory "buffers" or "decoys" for diverting intruding conspecifics and interspecific competitors from the residents' primary cavity, so that residents would be evicted less frequently at territories where birds defend extra nest-sites than at territories where birds defend one nest-site. Finally, (5) defense of extra nest-sites may be an example of superterritoriality (Harris 1979, 1985) whereby both males and females increase their inclusive fitness by preventing conspecifics from acquiring essential breeding resources (Verner 1977).

We address the hypotheses and predictions above by examining cases of extra nest-site defense by Tree Swallows breeding in nestbox and cavity populations. We describe the frequency, location, duration and outcome of cases of extra nest-site defense, and the characteristics and behaviour of residents defending extra nest-sites. We also report on two field experiments. The first involved the addition of extra boxes to test neighbour responses to a vacant nest-site. The second employed paired boxes to test the hypothesis that males or pairs would prefer a territory where two nest-sites could be easily defended, over one nest-site territories. Although there is some evidence that extra nest-sites may be used for reneesting, our results generally support the first hypothesis: male Tree Swallows exhibit resource defense polygyny (Emlen & Oring 1977) by defending extra nest-sites to attract secondary females, while females defend such nest-sites to prevent or delay the settlement of secondary females.

## METHODS

### Study sites

This study was conducted at five nestbox grids (BG, HU, NB, SP, HUB) in hayfields on research tracts of the Queen's University Biological Station, southeastern Ontario, Canada (44°34'N, 76°20'W), during 1985-1989, as well as two beaver ponds (Allan's Pond, Osprey Marsh) with many natural cavities, during 1986-1987. Each pond is located within 5 km of the nearest box

grids. In the grids, between 76 and 96 identical boxes mounted on aluminium poles were available for use each year. At HUB (established in 1986) boxes were 20 m from adjacent boxes along rows and columns and 28 m from the nearest box along the diagonal. At the four remaining grids, boxes were 40 m apart in rows and columns and 27 m from adjacent boxes along the diagonal. Nest-cavity density in the natural habitats, with a mean inter-cavity distance of 28 m, is remarkably similar to that in the grids (Robertson & Rendell 1990). The characteristics of each pond and the cavities in the natural populations are described in greater detail by Rendell & Robertson (1989) and Robertson & Rendell (1990).

#### Surveys, behavioural watches and nest checks

Surveys, behavioural watches, nest checks and chance observations enabled us to record: (1) nest-site occupancy, (2) cases of single and extra nest-site defense, (3) polygynous matings, (4) the duration of extra nest-site defense and the nesting stage during which it ended, (5) the fate of extra nest-sites and (6) the outcome of breeding attempts by pairs defending one or more nest-sites. We conducted surveys at weekly intervals at the grids in all five years, and on alternate days at the two natural cavity sites during 1986-1987. Surveys involved observing each nest-site until the identity of the male and female occupants could be verified. In the grids we checked nests every 1-3 days, and in the cavity populations, on alternate days in 1986 and daily in 1987. Nest-sites were considered occupied when defended by a pair of birds. We analyzed data only for those pairs that occupied nest-sites early in the season during the peak period of nest-site selection and settlement (i.e., before 1 June). The patterns of nest-site defense later in the season, after some nests have failed and there are few birds still settling, do not reflect the selective pressures on extra-site defense.

We did behavioural watches on pairs defending single and extra nest-sites from a canoe, hide, or vehicle, or at a distance >30 m, between 0530-1200 h, throughout four nesting stages (nest

building, egg laying, incubation, nestling) of the breeding cycle in both populations. Each watch was conducted using spotting scopes or binoculars, and involved continuous recording of the birds' behaviour for a period of 30 min to 1 h. For each watch we calculated the percentages of time spent on territories by both members of a pair, and the time contributed by males and females to defense of the primary and extra nest-sites. Defense was defined by presence on the nest-site. In the grids, birds typically could perch only on the primary or extra boxes, and not away from boxes, so it was obvious when a box was defended. Birds do not perch persistently on boxes that they cannot aggressively defend. In the cavity populations we assumed that residents were defending a cavity when they were perched <10 m from it. When residents perched >10 m from any cavity on their territory, they were assumed to be on the territory but not defending any particular nest-site. We summarized and analyzed data from behavioural watches conducted in 1987, the year during which we conducted the most watches in both grids ( $n = 77$  watches) and ponds ( $n = 117$  watches).

#### Capture and banding

In the grids we caught birds by hand, using mist nets, or box traps (Stutchbury & Robertson 1986), banded them and marked each one with non-toxic acrylic paints at conspicuous positions along the wing and tail. In the cavity populations we caught residents using cavity traps (Rendell *et al.* 1989) and temporary (2-3 h) erection of nest-boxes. When both members of a pair were unmarked in either population we distinguished individuals by differences in plumage colour and behaviour. We measured body mass (g) and wing length (mm) for all birds using Pesola (50 g) balances and rulers. Birds were sexed according to behavioural observations and morphological differences (Hussell 1983, Stutchbury & Robertson 1987b) and aged according to criteria in Hussell (1983) and using banding records. We were able to divide both males and females into four age groups for the purposes of analysis: after-hatch, after-second, after-third and after-fourth-year.

Relatively few birds were captured in the cavity populations, so we analyze the ages and physical characteristics of males and females from the grids alone.

### Experiment 1

To examine the response of neighbouring pairs to extra, unoccupied nest-sites, some nest-box sites were initially left vacant throughout all grids in 1985 ( $n = 14$ ) and 1986 ( $n = 22$ ). In 1985, seven boxes were erected in these vacant sites in early to mid-May and seven in early June, while in 1986, 22 boxes were erected in early to mid-May. Most pairs of swallows had settled at boxes and were nest building by early May. This did not alter the general arrangement of boxes described above, except in 1986 when five boxes were placed only 20 m from the nearest boxes along rows and columns. After erection of boxes on the vacant sites, we monitored the response of neighbouring males and females to the newly available nestbox.

### Experiment 2

To test whether Tree Swallows might prefer territories where they could easily defend two

nest-sites as opposed to one, we ascertained settlement dates of single birds (often known to be males) and dates when pairs first occupied territories with one or two nestboxes using early season scans (Rendell & Robertson 1990, Stutchbury & Robertson 1987c). At BG during 1987-1989 and HU in 1987-1988, half of the boxes (BG: 18/35 boxes, HU 9/18 boxes) were paired with an additional box placed 8 m away (hereafter "double box" territories), well within the usual territory size of Tree Swallows (Muldal *et al.* 1985). Territories with single or double boxes were situated alternately throughout each grid in each year of the experiment. If Tree Swallows preferred to defend territories where they could easily defend extra nest-sites, we predicted that settlement dates by single birds, and dates of pair formation, would be significantly earlier at territories with double boxes compared to those with only one box. Because double box territories were experimental, they were not included in any comparisons between extra nest-site defenses and single box territories unless stated otherwise.

**Table 1.** Percentage of pairs of Tree Swallows defending single box and double box territories, or one or more extra nest-sites, in the nestbox and cavity populations, 1985-1989.

	Year	No. of Pairs <sup>a</sup>	Percentage of all pairs in each defense category				
			Single	Double <sup>b</sup>	No. extra nest-sites <sup>c</sup>		
					1	2	3
Boxes	1985	(54)	83.3	-	16.7	0.0	0.0
	1986	(76)	73.7	-	25.0	1.3	0.0
	1987	(75)	52.0	32.0	13.3	0.0	2.7
	1988	(71)	56.3	25.4	5.6	9.9	2.8
	1989	(68)	63.2	7.4	16.2	4.4	8.8
Cavities	1986	(47)	61.7	-	29.8	8.5	0.0
	1987	(27)	48.1	-	44.4	3.7	3.7

<sup>a</sup>Total number of pairs for all grids or both cavity habitats combined. One observation per pair. <sup>b</sup>Double box sites were not available in 1985 and 1986, nor at the natural cavity habitats. See Methods, Experiment 2. <sup>c</sup>In the grids, includes pairs that defended single box or double box territories with extra nest-sites >8 m from the primary nest site.

**RESULTS**

**Defense of extra nest-sites**

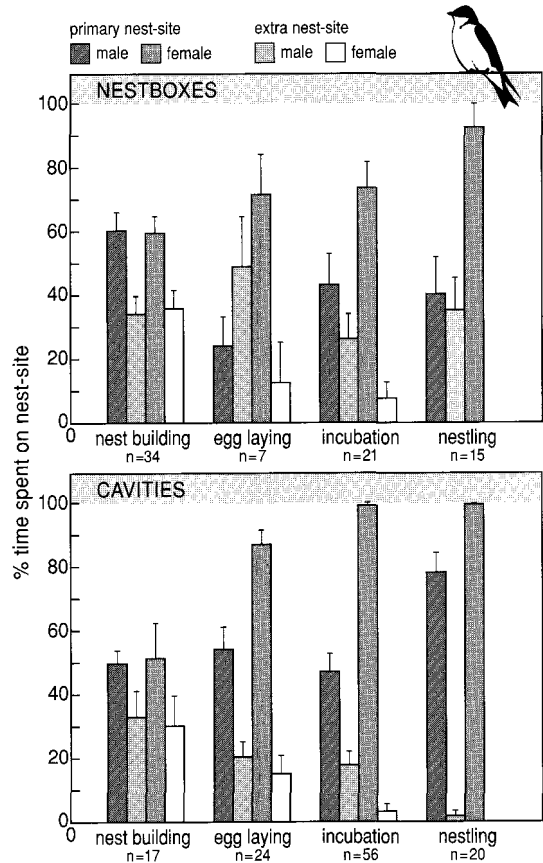
**Frequency** Defense of extra nest-sites by Tree Swallows occurs frequently. Each year approximately 15 to 29% of pairs in grids, and 38 to 52% of those in natural cavities, defended one or more extra nest-sites (Table 1). Typically, these territories included only one extra nest-site.

**Resident behaviour, age and physical characteristics**

Both males and females contributed to the defense of extra nest-sites in both populations (Fig. 1). On average, males devoted a greater proportion of the total time they spent on their territory to the defense of extra nest-sites than did females, significantly so during the incubation stage in both populations (Mann-Whitney Test, Boxes:  $z = 2.6$ , two-tailed  $p < 0.01$ ; Cavities:  $z = 4.3$ ,  $p < 0.0001$ ), and during the nestling stage in the grids ( $z = 3.3$ ,  $p < 0.01$ ). The time devoted by females to the defense of extra nest-sites dropped to zero by the nestling stage in both populations, while males devoted approximately one twentieth of the total time they spent on their territory to the defense of extra nest-sites throughout the nesting cycle.

The age distributions of males (Chi Square test,  $\chi^2 = 2.59$ ,  $df = 3$ ,  $p = 0.46$ ) and females ( $\chi^2 = 2.82$ ,  $df = 3$ ,  $p = 0.42$ ), were not different when comparing those defending single boxes versus those defending extra boxes.

Average body mass and wing length were not



**Fig. 1.** Percentages of time while on the territory spent at the primary and extra nest-sites by males and females. Data are for pairs of Tree Swallows defending extra nest-sites more than 8 m from the primary nest-site for both the nestbox and cavity populations during four stages of the nesting cycle. Values are means  $\pm$  SE;  $N$  = number of watches.

**Table 2.** Body mass (g) and wing length (mm) of males and females defending one or more nest-sites in the nest-box grids, 1985-1989. Values are means  $\pm$  SE,  $n$  = number of individuals in sample. Different letters denote that means are significantly different, Two-Sample  $t$ -test,  $t = 2.89$ ,  $df = 275$ , two-tailed  $p < 0.01$ .

Sex	Defense	Body mass	$n$	Wing length	$n$
Males	Extra	21.1 $\pm$ 0.2	55	119.7 $\pm$ 0.3	54
	Single	21.1 $\pm$ 0.1	162	119.3 $\pm$ 0.2	163
Females	Extra	20.8 $\pm$ 0.2	70	116.2 $\pm$ 0.3 <sup>a</sup>	70
	Single	21.0 $\pm$ 0.1	206	115.0 $\pm$ 0.2 <sup>b</sup>	207

significantly different between males defending one or more nest-sites in the grids (Table 2). Females defending extra nest-sites had significantly longer wings than those defending one nest-site, but the masses of females were not different between the two groups (Table 2).

**Location** In the nestbox grids, distances between primary boxes and extra nest-sites defended by Tree Swallows (range = 20-40 m) were similar to the range of distances observed in the cavity populations (range = 6.4-55.7 m, mean  $\pm$  SE,  $22.1 \pm 2.1$ ,  $n = 32$ ). The mean distance between primary and extra nest-sites in the cavity populations was calculated as the distance between the primary and most distant extra cavity.

Territories where pairs defended extra nest-sites were more likely to include one or more nest-sites at or near the edge of a grid or cavity population than expected by chance. In the nestbox populations, the edge of each colony or grid was defined by the nest-sites located along the periphery (see Fig. 1, Rendell & Robertson 1990), and in the cavity populations the edge of a colony was defined by the outermost, occupied cavities. To determine whether there was a tendency for cases of extra nest-site defense to be near the edge of colonies, we compared the number of extra nest-site territories having one or more of the nest-sites on the colony edge, with the number of those where none of the nest-sites defended by a pair were on the colony edge (i.e. all nest-sites were 'central'). This analysis was done for BG only because three of the remaining four grids are small, and consequently all of the nestboxes on those grids are on the edge. At HU no pairs defended extra nest-sites more than 8 m from a primary nest-site. We determined the expected ratio of extra nest-site defenses (wholly central versus partly or wholly on the edge) by counting all possible combinations of extra nest-site defenses in BG where one or two extra nest-sites could be defended. The expected ratio was approximately 1:1 (83 possible territories with extra defenses centrally located to 76 with at least one nest-site on

the grid edge). Therefore, we used a binomial probability distribution to analyze the observed frequency of defenses with extra nest-sites at these locations in a grid, for all extra nest-site defenses combined from five years of data at BG. Significantly more defenses of extra nest-sites at BG included at least one extra nest-site at the grid edge ( $n = 25$ ) than where all boxes were central to the grid edge ( $n = 8$ ; Binomial Test, two-tailed  $p = 0.002$ ). This analysis was not possible in the cavity populations because we could not estimate an expected ratio. In the cavity populations in 1987, four (28.6%) extra nest-site defense territories included only nest-sites central to the colony edge, and ten (71.4%) included at least one nest-site on the edge. In 1986 an equal number of extra nest-site defenses included one nest-site on the colony edge ( $n = 9$ , 50%), or were wholly central to the colony edge ( $n = 9$ , 50%).

**Duration** On average, resident pairs in the grids defended extra nest-sites for over one month (mean  $\pm$  SE,  $38.3 \pm 2.4$  days,  $n = 74$ , range = 1-89 days), significantly longer than pairs in the cavity populations, which defended extra nest-sites for approximately three weeks ( $20.1 \pm 2.5$  days,  $n = 32$ , range = 1-63 days; Mann-Whitney Test,  $z = 4.2$ , two-tailed  $p < 0.0001$ ). Consequently, extra nest-site defenses ended significantly later in the nesting cycle for pairs in the grids compared to those in the cavity populations (Table 3). Over one half of the cases of extra nest-site defense in the grids lasted beyond the incubation stage, whereas in the cavity populations, over one half of these cases ended prior to the incubation stage.

**Fate of extra nest-sites** The fates of extra nest-sites were different between nestbox and cavity populations (Table 3). In the grids, polygyny occurred at approximately one quarter of the territories where pairs defended extra nest-sites, while polygynous matings were not observed in the cavity populations. On two occasions males became polygynous on the experimental double box territories. No male defending a single box attracted a second female to nest on the territory si-

**Table 3.** Percentage of pairs reaching various nesting stages in the primary nests before defense of extra nest-sites ended, and the fate of extra nest-sites, at the nestbox and cavity populations, 1985-1989. Number of cases of extra nest-site defense in brackets. Totals were combined across grids, ponds, and years for both populations. The distributions were different when comparing nestbox and cavity populations for both the stage at which extra nest-site defense ended and the fate of the extra nest-site (Stage  $\chi^2 = 17.4$ ,  $df = 4$ ,  $p = 0.002$ ; Fate  $\chi^2 = 24.2$ ,  $df = 5$ ,  $p < 0.001$ ).

	Percentage of pairs	
	Nestboxes (74)	Cavities (32)
Stage extra nest-site defense ended		
Nest building	24.3	56.2
Egg laying	6.8	0
Incubation	17.6	28.1
Nestling	31.1	12.5
Fledging	20.3	3.1
Fate of extra nest-site <sup>a</sup>		
Not used	18.9	18.8
Entire territory abandoned	17.6	28.1
Usurped by conspecifics	24.3	12.5
Usurped by other species	13.5	25.0
Polygyny	25.7	0
Pair renested in extra site	0	15.6

<sup>a</sup>Fates of only one extra nest-site per defense.

multaneously with the primary female. Conspecific and interspecific competitors (Rendell & Robertson 1989, 1990, 1991; Robertson & Rendell 1990) usurped extra nest-sites from residents in both grid and cavity populations, but conspecific usurpations were more common in the grids, and interspecific usurpations were more common in the cavities. In a few cases, extra nest-sites were either abandoned when the entire territory was abandoned, or they were simply not used.

After failure of their first breeding attempt, five resident females renested in their extra nest-site in the natural populations (Table 3). However, this was not observed in the grids where only two females involved in extra nest-site defenses renested after a failed breeding attempt, and these females reused the same box. Further, seven females defending only one box renested and each in the same nest-site as the one used in the first breeding attempt. This suggests that the defense

of extra nest-sites is not essential for renesting, although an extra nest-site may be useful if the first site is rendered inferior due to the failure.

**Usurpation of primary nest-sites and resident evictions** The likelihood of eviction and replacement of one or both residents from the primary nest-site was the same, regardless of whether a pair was defending a single nest-site or defending two or more nest-sites, in both the nestbox (2 x 2 Contingency Tables,  $\chi^2 = 0.055$ ,  $df = 1$ ,  $p = 0.82$ ) and cavity populations ( $\chi^2 = 2.152$ ,  $df = 1$ ,  $p = 0.142$ ). Our prediction was that pairs defending extra nest-sites would more likely be evicted from the primary nest-site than pairs defending a single nest-site would be loose it. The time spent defending the extra site would make the primary nest-site more vulnerable and also there would be a lower cost associated with the loss of the primary site because the pair could resort to using

the extra nest-site. In the grids one or both residents were evicted by conspecifics or competitors on 22 occasions at single defense territories ( $n = 223$  total territories) and eight occasions at extra nest-site defense territories ( $n = 74$ ). In the cavity populations, these evictions occurred six and nine times, at single ( $n = 42$ ) and extra nest-site defense ( $n = 32$ ) territories, respectively.

### Experiment 1

Sixty percent of all boxes erected after females had begun nesting were defended by neighbouring established pairs (1985: 5/7 (71%) early season box additions and 2/7 (29%) late season box additions; 1986: 15/22 (68%) box additions). The remainder of the added boxes were either settled and defended as lone boxes by pairs new to the grids (1985: 2/7 (29%) of the remaining early and late box additions combined; 1986: 6/22 (27%) box additions), or were left unoccupied.

In 1985 and 1986, respectively, polygynous matings occurred at 71% (5/7) and 20% (3/15) of the territories where added boxes were defended by established pairs.

### Experiment 2

Both male and pairs of Tree Swallows showed a preference for territories where they could easily defend two boxes as opposed to one. Settlement dates by single birds (often known to be males) at territories with paired boxes in BG, and the dates when pairs occupied territories in HU,

were significantly earlier than those at territories with single boxes (Table 4).

## DISCUSSION

A large proportion of pairs of Tree Swallows defended at least one extra nest-site for approximately one month or longer, in both the nestbox and cavity populations during each year of the study. Unlike observations in Harris (1979), Tree Swallows did not simply defend extra nest-sites close to their primary nest but, in the natural populations, traveled up to 56 m to defend an extra nest-site. Also, pairs specifically oriented their territory to encompass a particular neighbouring nest-site rather than simply defending circular territories as described by Robertson & Gibbs (1982). In the grids, all nestboxes had from two to four neighbouring nestboxes within 28 m. It was obvious that pairs defending extra boxes occupied oblong territories rather than circular ones which would have encompassed several extra nest-sites. Both resident males and females participated in defense of the extra nest-sites, although males spent more time at the extra nest-sites than females during later stages of the nesting cycle.

Experiment 1 showed that many settled pairs will expand their territory to defend extra, proximate nest-sites that become available later in the season. Experiment 2 showed that male Tree Swallows prefer territories where the defense of

**Table 4.** Settlement dates of single birds and pairs at territories with one nestbox and those with paired nestboxes at HU and BG grids during Experiment 2, 1987-1989.

Grid	Territory	Single birds	Pairs of birds	<i>n</i>
HU	Paired boxes	5 April $\pm$ 1.1	8 April $\pm$ 1.2 <sup>a</sup>	17
	One box	8 April $\pm$ 2.0	13 April $\pm$ 2.1 <sup>b</sup>	18
BG	Paired boxes	8 April $\pm$ 1.2 <sup>a</sup>	14 April $\pm$ 0.9	38
	One box	12 April $\pm$ 1.3 <sup>b</sup>	16 April $\pm$ 1.0	43

Values are means  $\pm$  SE,  $n$  = number of territories.

Different letters denote that means are significantly different. HU:  $t$  (corrected for unequal variances) = 2.14,  $df$  = 24,  $p$  = 0.002; BG:  $t$  = 2.40,  $df$  = 79,  $p$  < 0.001.



extra nest-sites is readily possible, and there is some evidence that pair formation, or at least settlement by pairs, occurs preferentially in situations where two nest-sites can be easily defended. However, this experiment does not provide a clear test of female preference for one versus two nest-site territories, because in some cases pair formation appears to precede settlement, and female choice is dependent on availability of males of different status. Corroborating results in Mitchell (1992), our observations of the active defense of extra nest-sites suggests that their occupation by Tree Swallows does not arise due to the passive avoidance of nest-sites near nesting conspecifics thereby leaving some nest-sites undefended. Our results indicate extra nest-sites serve one or more adaptive functions and are actively sought out and defended. Below, we examine the function of extra nest-site defense and we interpret our data from the viewpoint of the male, female and pair.

(1) By defending extra nest-sites, male Tree Swallows improve the likelihood of attracting a second female. Similar results were found previously for Tree Swallows (Dunn & Hannon 1991) and other cavity nesters including Prothonotary Warblers *Protonotaria citrea* (Petit 1991) and House Wrens *Troglodytes aedon* (Johnson & Kermott 1991). In our study, one quarter of male Tree Swallows defending extra nest-sites became polygynous, whereas no males defending lone nest-boxes attracted a second female. Farber (1972), Quinney (1983) and Rendell (1992) have described cases of polygyny in Tree Swallows involving two females nesting simultaneously in the same nestbox, but these are rare events.

Polygynous males do not, on average, fledge more young than monogamous males in our populations. Secondary females usually cannot provide enough food to fledge young without male help (Dunn & Robertson 1992, Leffelaar & Robertson 1986), and males rarely assist a secondary female with raising her brood, as long as the primary female's brood is more advanced. However, in areas where food is abundant, females are more likely to fledge young without male assistance,

and polygynous male Tree Swallows in Alberta fledge up to twice as many young as males with one female (Dunn & Hannon 1991). The potential for greater reproductive output for polygynous than monogamous males may be sufficient to selectively favour a mating system of resource defense polygyny (Emlen & Oring 1977) and, therefore, extra nest-site defense for the purpose of attracting a second female.

While males may defend extra nest-sites to attract a second female, resident females may defend the same extra nest-sites to prevent or delay settlement of a second female. The relatively low cost of chasing intruding females from the extra nest-site is probably offset by the reduced probability of losing the male's assistance in rearing the brood. By preventing the settlement of a second female at an extra nest-site, or by reducing the temporal overlap between breeding attempts of primary and secondary females on the same territory, resident females might secure the complete aid of their mate (Arcese 1989, Hannon 1984, Slagsvold & Lifjeld 1994, Whittingham 1989). Although primary females generally receive all of the male's assistance and hence suffer no disadvantage due to the presence of a secondary female, a primary female might easily become secondary in terms of nesting chronology if she is delayed or if her first attempt fails. By preventing a second female from settling, or at least delaying her, the primary female reduces the risk that she herself will drop to secondary status.

Selection for polygyny and extra nest-site defense might also occur if males with two females were less likely to lose both broods to predation or stochastic nest failure than monogamous males were to lose their only brood. Use of cone-shaped guards at our boxes effectively eliminates predation, so our results do not provide a test of this hypothesis. However, we do know that predation in cavity populations is relatively common (Robertson & Rendell 1990), so polygyny, where it occurs in natural habitats, may result in a higher reproductive success for polygynous males, even when secondary females cannot raise young without male assistance.

It is somewhat surprising that we did not observe polygyny in the natural populations. It has been hypothesized that polygyny in some species could be an artifact of an abundance of suitable nest-sites in nestbox populations (Alatalo & Lundberg 1984) and naive secondary females (Petit 1991). However, in a study of House Wrens, Johnson & Kermott (1991) discredited these hypotheses by showing that male wrens actively solicit second females to their territory, and become polygynous in natural habitats, albeit at a lower frequency compared to wrens in box populations. Male Tree Swallows in natural habitats defend extra nest-sites, so some cases of polygyny undoubtedly occur there, but our results indicate its frequency is much lower than in the grids.

(2) Surplus nest-sites could improve mate retention by serving as renesting sites for resident males and females when an earlier breeding attempt fails. Mate retention was improved for male Pied Flycatchers *Ficedula hypoleuca* that defended extra nest-sites after early breeding failure (Slagsvold & Lifjeld 1986). Females may switch nest-sites to renest because one nest failure (e.g., brood death, predation) may indicate the likelihood of future failure, or because failure of the first attempt may have reduced the quality of the primary cavity if, for example, the dead nestlings cannot be removed or if the cavity is torn open by a predator. Indeed, females in the cavity populations renested in extra nest-sites when possible, although females renesting in the grids always used their original nest-site, even when they had access to extra nest-sites. Nevertheless, defense of an extra nest-site is not essential for mate retention. In all cases where females renested in the cavity and nestbox populations, whether defending one or more nest-sites, the same male and female remained together for the second attempt. It remains possible, however, that defense of an extra nest-site is advantageous to ensure a renesting opportunity, especially in natural cavity populations which suffer more predation than in the protected nestbox populations.

(3) The defense of extra nest-sites by males may reflect male quality and, therefore, affect

mate choice (Slagsvold & Lifjeld 1986). However, as with Prothonotary Warblers (Petit 1991), male Tree Swallows defending extra nest-sites were not different in their mass, wing length or age from males defending single nest-sites. Yet our Experiment 2 suggested that females may settle preferentially with males defending extra nest-sites. Petit (1991) also found that female Prothonotary Warblers settled earlier with males that defended extra nest-sites. This preference could occur if these were better territories, rather than that they were occupied by higher quality males. Slagsvold (1986) showed that female Pied Flycatchers chose to nest with males based on the quality of their territory and not their phenotype.

The spatial distribution of extra nest-site defense is not consistent with the hypothesis that these are defended by higher quality males. Instances of extra nest-site defense in both the nestbox and natural cavity populations were often observed to be located on or near the edge of a colony, an area that settling Tree Swallows typically avoid due to increased interspecific competition for nest-sites and increased predation (Rendell & Robertson 1990). Perhaps all males seek to defend one or more extra cavities at the time they settle, but many males are prevented from doing so due to increased intraspecific competition for nest-sites in high quality locations (e.g. central in a population). On the other hand, it is possible that the benefits of securing an extra nest-site even in a marginal part of the nesting area are higher than the costs of having the primary nest-site in marginal habitat.

Although our results do not indicate that males which defend extra nest-sites are higher quality than those that defend only one site, there is a suggestion that by defending extra nest-sites, male Tree Swallows may attract higher quality females. Females defending extra nest-sites in the grids were larger than those defending lone sites. Alternatively, in those cases where birds are paired at the time of settling, it may be that males which have larger mates are more likely to defend an extra nest-site.

(4) Our observations do not support the hy-

pothesis that pairs defend extra nest-sites because they act as "decoys" or "buffers" which deter competitors from evicting and replacing resident individuals or pairs from a primary nest-site (Robertson & Gibbs 1982). Competitors evicted and replaced residents at primary nest-sites as often on territories where extra nest-sites were being defended as at single defense territories.

(5) Defense of extra nest-sites by Tree Swallows has been interpreted as an example of superterritoriality (Harris 1979, 1985) which, in the absence of either direct benefits or costs from the defense of resources not essential for breeding (Colgan 1979, Getty 1979, Pleasants & Pleasants 1979, Rothstein 1979), is a spiteful behaviour that improves an individual's relative fitness by diminishing others'. However, our study and others (Dunn & Hannon 1991, Dunn & Robertson 1992) have demonstrated potential benefits of this behaviour, and there are costs to aggression in Tree Swallows (Leffelaar & Robertson 1985, Lombardo 1986a, Robertson *et al.* 1986). Consequently, superterritorial behaviour would not evolve in this species.

### Why do Tree Swallows defend extra nest-sites?

Extra nest-site defense by Tree Swallows is a relatively common form of territorial behaviour that affords males an opportunity for bigamy, and hence, the potential for greater reproductive success. Extra nest-sites may also be advantageous for ensuring availability of a breeding opportunity if the first nest is destroyed. Because males stand to gain the most from defense of alternate nest-sites, it is not surprising that males spend more time than females at the secondary nest-sites in their efforts to attract another mate. This raises the question: are females willing participants in defense of extra nest-sites, or are they engaged in female-female competition for the sole attention and parental care of males (cf. Leffelaar & Robertson 1986)? Females do spend time at secondary nest-sites in the absence of intruders (e.g., exploring a cavity), but once a choice of primary nest-site is made, are females defending the extra site to maintain the alternate cavity or to keep sec-

ondary females away? We suggest that female defense of extra nest-sites is for the primary purpose of preventing other females from settling. In our populations, female success is dependent upon male parental care (Leffelaar & Robertson 1986), and secondary females are threats not only to male attention, but also to the primary nest-site (Leffelaar & Robertson 1985, Dunn & Hannon 1991). Thus a conflict of interest exists between the sexes with both members of a pair trying to achieve maximum reproductive success. For male Tree Swallows, the extended defense of extra nest-sites throughout the breeding cycle to a stage when the primary female is otherwise occupied (i.e., the incubation stage) may reduce female-female competition at a territory, thereby increasing the likelihood that a second female may settle.

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### REFERENCES

- Alatalo R.V. & A. Lundberg 1984. Polyterritorial polygyny in the Pied Flycatcher *Ficedula hypoleuca* - evidence for the deception hypothesis. *Ann. Zool. Fenn.* 21:217-228.
- Arcese, P. 1989. Intrasexual competition and the mating system in primarily monogamous birds: the case of the Song Sparrow. *Anim. Behav.* 38:96-101.

- Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-169.
- Colgan, P. 1979. Is a superterritorial strategy stable? *Am. Nat.* 114:604-605.
- Dunn, P.O. & S.J. Hannon 1991. Intraspecific competition and the maintenance of monogamy in Tree Swallows. *Behav. Ecol.* 2:258-266.
- Dunn, P.O. & R.J. Robertson 1992. Geographic variation in the importance of male parental care and mating systems in Tree Swallows. *Behav. Ecol.* 3:291-299.
- Emlen, S.T. & L.W. Oring 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- Farber, H. 1972. Evidence of two Tree Swallow females sharing the same nest box. *Wilson Bull.* 84:204.
- Getty, T. 1979. On the benefits of aggression: the adaptiveness of inhibition and superterritories. *Am. Nat.* 114:605-609.
- Hannon, S.J. 1984. Factors limiting polygyny in the Willow Ptarmigan. *Anim. Behav.* 32:153-161.
- Harris, R.N. 1979. Aggression, superterritories and reproductive success in Tree Swallows. *Can. J. Zool.* 57:2072-2078.
- Harris, R.N. 1985. Territoriality in Tree Swallows. *Condor* 87:566.
- Holroyd, G.L. 1975. Nest site availability as a factor limiting population size of swallows. *Can. Field-Nat.* 89:60-64.
- Hussell, D.J.T. 1983. Age and plumage color in female Tree Swallows. *J. Field Ornithol.* 54:312-318.
- Johnson, L.S. & L.H. Kermott 1991. Effect of nest-site supplementation on polygynous behavior in the House Wren (*Troglodytes aedon*). *Condor* 93:784-787.
- Leffelaar, D. & R.J. Robertson 1985. Nest usurpation and female competition for breeding opportunities by Tree Swallows. *Wilson Bull.* 97:221-224.
- Leffelaar, D. & R.J. Robertson 1986. Equality of feeding roles and the maintenance of monogamy in Tree Swallows. *Behav. Ecol. Sociobiol.* 18:199-206.
- Lombardo, M.P. 1986a. A possible case of adult intraspecific killing in the Tree Swallow. *Condor* 88:112.
- Lombardo, M.P. 1986b. Attendants at Tree Swallow nests. I. Are attendants helpers at the nest? *Condor* 88:297-303.
- Mitchell, J. 1992. Multiple nest site defense in the Tree Swallow (*Tachycineta bicolor*). (B.Sc. thesis). Kingston: Queen's University.
- Muldal, A., H.L. Gibbs & R.J. Robertson 1985. Preferred nest spacing of an obligate cavity-nesting bird, the Tree Swallow. *Condor* 87:356-363.
- Petit, L. 1991. Experimentally induced polygyny in a monogamous bird species: Prothonotary Warblers and the polygyny threshold. *Behav. Ecol. Sociobiol.* 29:177-187.
- Pleasants, J.M. & B.Y. Pleasants 1979. The superterritory hypothesis: a critique, or why there are so few bullies. *Am. Nat.* 114:609-614.
- Quinney, T.E. 1983. Tree Swallows cross a polygyny threshold. *Auk* 100:750-754.
- Rendell, W.B. 1992. Peculiar behavior of a subadult female Tree Swallow. *Wilson Bull.* 104:756-759.
- Rendell, W.B. & R.J. Robertson 1989. Nest-site characteristics, reproductive success and cavity availability for Tree Swallows breeding in natural cavities. *Condor* 91:875-885.
- Rendell, W.B. & R.J. Robertson 1990. Influence of forest edge on nest site selection by Tree Swallows. *Wilson Bull.* 102:634-644.
- Rendell, W.B. & R.J. Robertson 1991. Competition for natural cavities among Great Crested Flycatchers, *Myiarchus crinitus*, Northern Flickers, *Colaptes auratus*, and Tree Swallows, *Tachycineta bicolor*. *Can. Field-Nat.* 105:113-114.
- Rendell, W.B., B.J. Stutchbury & R.J. Robertson 1989. A manual trap for capturing hole-nesting birds. *N. Am. Bird Bander* 14:109-111.
- Robertson, R.J. & H.L. Gibbs 1982. Superterritoriality in Tree Swallows: a reexamination. *Condor* 84:313-316.
- Robertson, R.J., H.L. Gibbs & B.J. Stutchbury 1986. Spitefulness, altruism, and the cost of aggression: evidence against superterritoriality in Tree Swallows. *Condor* 88:104-105.
- Robertson, R.J. & W.B. Rendell 1990. A comparison of the breeding ecology of a secondary cavity-nesting bird, the Tree Swallow (*Tachycineta bicolor*), in nest boxes and natural cavities. *Can. J. Zool.* 68:1046-1052.
- Robertson, R.J., B.J. Stutchbury & R.R. Cohen 1992. Tree Swallow. In: A. Poole, P. Stettenheim & F. Gill (eds). *The Birds of North America*, No. 11 Philadelphia: The Academy of Natural Sciences; Washington, DC: The American Ornithologists' Union.
- Rothstein, S.L. 1979. Gene frequencies and selection for inhibitory traits, with special emphasis on the adaptiveness of territoriality. *Am. Nat.* 113:317-331.
- Slagsvold, T. 1986. Nest site settlement by the Pied Flycatcher: does the female choose her mate for the quality of his house or himself? *Ornis. Scand.* 17:210-220.
- Slagsvold, T. & J.T. Lifjeld 1986. Mate retention and male polyterritoriality in the Pied Flycatcher *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.* 19:25-30.

- Slagsvold, T. & J.T. Lifjeld 1988. Why are some birds polyterritorial? *Ibis* 130:65-68.
- Slagsvold, T. & J.T. Lifjeld 1994. Polygyny in birds: the role of competition between females for male parental care. *Am. Nat.* 143:59-94.
- Stutchbury, B.J. 1991. Coloniality and breeding biology of Purple Martins (*Progne subis hesperia*) in saguaro cacti. *Condor* 93:666-675.
- Stutchbury, B.J. & R.J. Robertson 1985. Floating populations of female Tree Swallows. *Auk* 102:651-654.
- Stutchbury, B.J. & R.J. Robertson 1986. A simple trap for catching birds in nest boxes. *J. Field Ornithol.* 57:64-65.
- Stutchbury, B.J. & R.J. Robertson 1987a. Behavioural tactics of subadult female floaters in the Tree Swallow. *Behav. Ecol. Sociobiol.* 20:413-419.
- Stutchbury, B.J. & R.J. Robertson 1987b. Two methods of sexing adult Tree Swallows before they begin breeding. *J. Field Ornithol.* 58:236-242.
- Stutchbury, B.J. & R.J. Robertson 1987c. Do nest building and first egg dates reflect settlement patterns of females? *Condor* 89:587-593.
- Stutchbury, B.J. & R.J. Robertson 1987d. Signaling subordinate and female status: two hypotheses for the adaptive significance of subadult plumage in female tree swallows. *Auk* 104:717-723.
- Verner, J. 1977. On the adaptive significance of territoriality. *Am. Nat.* 111:769-775.
- Von Haartman, L. 1957. Adaptation in hole-nesting birds. *Evolution* 11:339-347.
- Von Haartman, L. 1969. Nest-site and evolution of polygamy in European passerine birds. *Ornis Fenn.* 46:1-12.
- Whittingham, L.A. 1989. An experimental study of parental care in Red-winged Blackbirds. *Behav. Ecol. Sociobiol.* 25:73-80.

## SAMENVATTING

De (Noordamerikaanse) Boomzwaluw maakt onder normale omstandigheden een nest in een boomholte, maar accepteert ook nestkasten. Ongeveer 50% van de paren die in een experimentele populatie werd onderzocht, verdedigde extra nestelplaatsen gedurende een maand of langer tot op meer dan 50 meter van het nest. De extra plek werd door beide seksen verdedigd, maar de mannetjes besteedden daar meer tijd aan, vooral later in het seizoen (Fig. 1).

In een eerste experiment werden nestkasten opgehangen naast een bezette kast. Liefst 60% van de nieuwe kasten werd in bezit genomen door een naburig paar. In een tweede experiment kon worden vastgesteld dat Boomzwaluwen bij vestiging van een territorium een voorkeur hebben voor plaatsen met twee kasten boven die met slechts één.

Er waren geen aantoonbare leeftijdsverschillen tussen de zwaluwen die al dan niet een extra nestplaats verdedigden, en ook geen verschillen in lichamelijke eigenschappen van de mannetjes, maar bij de wijfjes bleek dat wel het geval te zijn. Wijfjes met extra nestplaatsen hadden langere vleugels.

Een extra nestplaats kan voordeel hebben in het geval dat een predator het nest vernield, maar meestal werden de extra nestplaatsen niet gebruikt als er een vervolgegsel werd geproduceerd. Een extra nestplaats bleek ook geen voordelen te bieden bij de verdediging van een territorium. Het belangrijkste voordeel lijkt de mogelijkheid voor mannetjes om een extra wijfje aan te trekken.

Hoewel polygynie onbekend is in natuurlijke populaties van deze soort, bleken sommige mannetjes in de experimentele populaties daartoe wel degelijk in staat. De functie van de rol van het wijfje bij de verdediging van de extra nestplaatsen zou kunnen berusten op het verhinderen of uitstellen van vestiging door andere wijfjes.

JvR