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NEST-SITE CHARACTERISTICS, REPRODUCTIVE SUCCESS AND CAVITY AVAILABILITY FOR TREE SWALLOWS BREEDING IN NATURAL CAVITIES[1]

WALLACE B. RENDELL AND RALEIGH J. ROBERTSON
Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

Abstract. We examined 10 characteristics of natural cavities and their influence on reproductive success of Tree Swallows (*Tachycineta bicolor*) nesting in dead trees in beaver ponds. Large ranges were found for entrance height and area, cavity volume, and nearness to shore of nest sites. Other characteristics were less variable: 46% of cavities were less than 2 m above the pond surface, and 48% had entrance widths of 4–5 cm. Tree Swallow nest sites were uniformly dispersed in the ponds.

Two cavity characteristics, cavity height and floor area, influenced reproductive success. Lower nest sites were more frequently preyed on and females laid larger clutches in cavities with a large floor area.

Five species larger than Tree Swallows used cavities during the study. Girth of the snag at the base and at the cavity, entrance width, and cavity volume were significantly greater at sites used by these species than those used by Tree Swallows.

Nest sites suitable for breeding did not appear to be limiting to Tree Swallows, because characteristics of unused cavities did not differ from those used by Tree Swallows and other species. Intraspecific territoriality was likely responsible for the large number of unused cavities in our populations. Other factors influencing cavity availability in our sites include interspecific competition, predation, snag fall, and continuing woodpecker excavation.

Key words: Natural cavities; reproductive success; cavity availability; Tree Swallows; Tachycineta bicolor.

INTRODUCTION

Characteristics of cavity nest sites are important determinants of occupation by secondary hole-nesting birds. Macrohabitat variables such as tree species diversity and density (e.g., Swallow et al. 1986) and canopy height (e.g., McCallum and Gehlbach 1988) influence nest-site use. This is also true of microhabitat variables. Van Balen et al. (1982) showed that several characters, including cavity height and volume, and entrance diameter, determined cavity use by European Starlings (*Sturnus vulgaris*), Great Tits (*Parus major*), and Blue Tits (*Parus caeruleus*) in northern Europe.

Nest-site characters also influence reproductive parameters of secondary cavity-nesters and, as a result, may be the most important criteria in female mate choice for these birds (Alatalo et al. 1986). Increasing the volume of nest boxes in experimental studies has resulted in larger clutches for nesting pairs in some species (e.g., Karlsson and Nilsson 1977), but not in others (e.g., Pitts 1988). Also, predation rates were found to be greater at nest sites that were closer to the ground for four passerine species in Europe (Nilsson 1984a).

Nest sites suitable for breeding are thought to be limiting for many secondary hole-nesting species (von Haartman 1957). Many studies have supported this hypothesis (for Tree Swallows *Tachycineta bicolor,* Holroyd 1975, Stutchbury and Robertson 1987b, cf. Snyder 1977). However, others (e.g., van Balen et al. 1982, Ingold and Ingold 1984, Peterson and Gauthier 1985) report an abundance of unoccupied and conceivably suitable cavities. Little has been done to examine the extent to which natural cavity nest sites are limiting to a particular breeding population and the factors that influence the occupancy and availability of suitable nest sites (cf. Snyder 1977).

We examined the nest-site characteristics of Tree Swallows during a comparative study of their breeding ecology in natural cavities and nest-box populations (Rendell 1987). Tree Swallows have been studied extensively in nest-box populations (e.g., Kuerzi 1941, DeSteven 1980, Hussell and Quinney 1987, Stutchbury and Robertson 1988) but little is known about their ecology in a natural habitat (cf. Erskine and McLaren

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1976, Peterson and Gauthier 1985). In this study, we provide the first detailed description of the cavity nest sites occupied by Tree Swallows, and an assessment of their influence on measures of reproductive success. We also compare nest sites of Tree Swallows with those of other species, and with unoccupied cavities in the same habitat to determine if cavities are limiting. Finally, we discuss the factors that influence cavity availability in our populations.

METHODS

STUDY SITES

This study was conducted in 1986 and 1987 near the Queen's University Biological Station, 50 km north of Kingston, Ontario, Canada. The study sites, Allan's Pond (AP) and Osprey Marsh (OM), are woodlands flooded by beaver dams. The two sites are 8 km apart. Hundreds of snags (dead trees) remain standing in water at each site. These snags are excavated by woodpeckers for nesting and roosting and the excavations are subsequently occupied by Tree Swallows and other species. AP is 4 ha with snags distributed evenly throughout the pond. OM is 11 ha with most snags clumped in the south-central part of the pond. The northern half of OM is covered in cattail beds. Water levels in both ponds fluctuate substantially each year due to dam quality and rainfall (mean depths = 0.5–1.5 m). The catchment about each pond is deciduous woodland consisting primarily of maple (*Acer* spp.), oak (*Quercus* spp.), poplar (*Populus* spp.), and basswood (*Tilia* spp.). The standing snags at each site were most likely of these species.

GENERAL METHODS

Cavities occupied by Tree Swallows and other species were located by surveys from canoe conducted daily throughout the breeding season. Nest cavities were considered active if the cavity was defended or if nest building was observed. Snags with active nests were marked with aluminum tags engraved with the site code and cavity number, and each site was mapped to scale.

NEST-SITE CHARACTERISTICS

Cavity and snag characteristics of nest sites used in 1986 only were measured during January–February 1987, when the ponds were frozen. Some further measurements of snags were made in March and July 1989. In 1986, Tree Swallows used 52 cavities for 64 breeding attempts (eight cavities were used two times, two cavities were used three times). We measured 48 of these nest sites (48/52 = 92%; four snags fell between summer and winter). We also measured 20 nest sites of 38 (53%) occupied by interspecific competitors combined for both sites, along with 19 cavities not occupied in 1986. These cavities were chosen randomly from an estimated 78 cavities that were unoccupied for both sites combined in 1986 (19/78 = 25%). A 7-m extension ladder stabilized by three guy ropes, similar to that subsequently described by Rohwer (1988), was used to gain access to cavities.

The following measurements were obtained for all cavities: total snag height (estimated for snags >8 m), the height of the cavity above the water (measured to the bottom edge of the entrance), entrance height, entrance width, girth of the snag base, and girth of the snag at the cavity. Distance to the nearest nesting conspecific and distance to the nearest shore were measured for Tree Swallow cavities. Distance to nearest Tree Swallow pair was also measured for the unoccupied cavities of 1986.

Cavity depth, from the bottom edge of the entrance to the cavity floor, and cavity width, from the entrance to the back wall of the cavity, were measured using a weighted measuring tape and ruler. These variables were used to estimate cavity volume. Cavity shape was assumed to be cylindrical. Entrance area was calculated for all measured cavities by the equation for an ellipse and the equation for the area of a circle was used to calculate floor area.

REPRODUCTIVE SUCCESS

In 1986 and 1987, behavioral watches and nest checks were conducted daily to examine nest contents, and determine the nesting stage and outcome of breeding attempts by Tree Swallows. Nest contents were seen using the naked eye and mirrors. Clutch size and other breeding parameters were recorded for accessible nests (to 3.0 m). Nest contents of higher cavities were not monitored because decay had weakened the snags thereby preventing climbing. For inaccessible cavities, the nesting stage and outcome of a breeding attempt were estimated by surveys and behavioral watches.

RESULTS

NEST-SITE CHARACTERISTICS

Tree Swallows. The characteristics of nest sites used by Tree Swallows had broad ranges (Fig. 1,

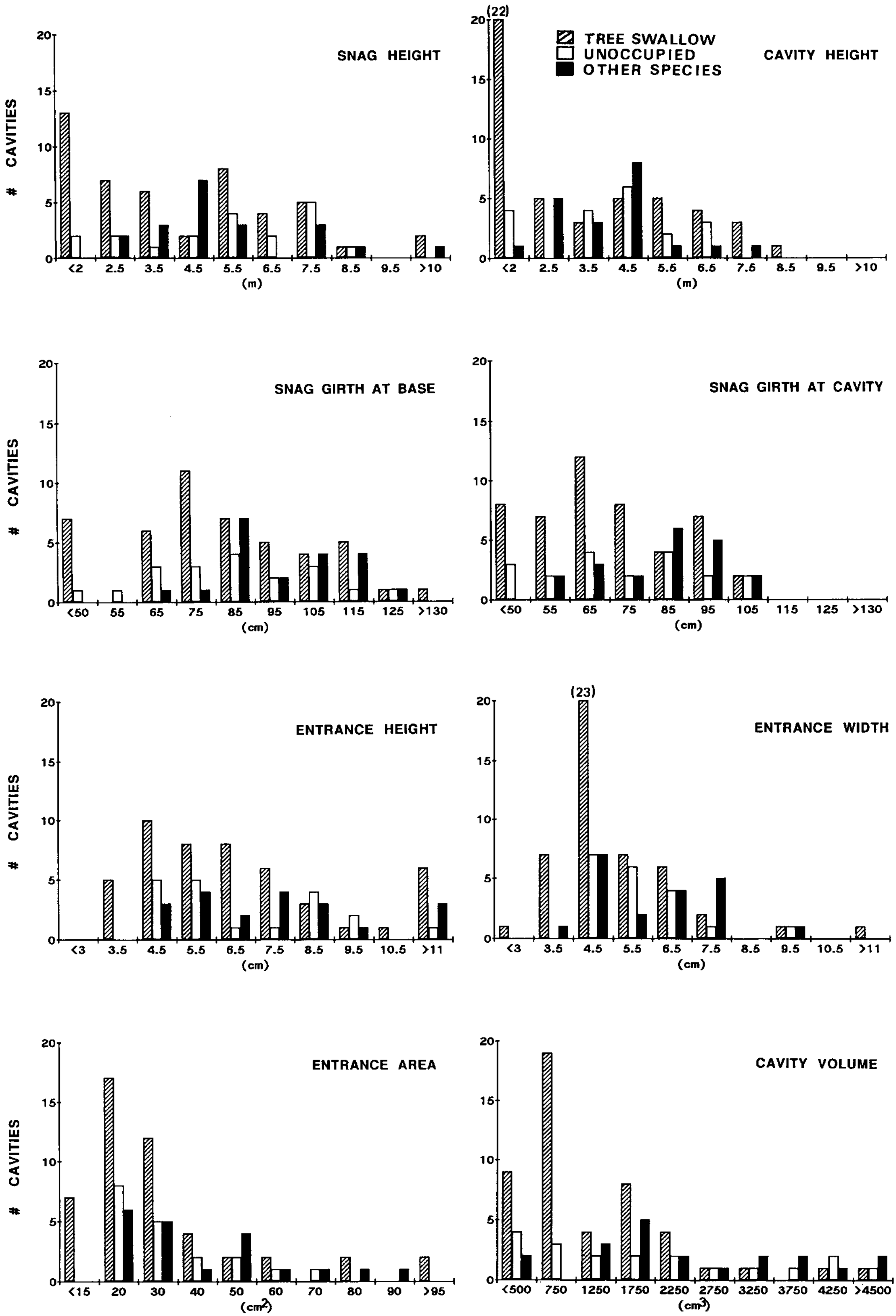

FIGURE 1. Frequency distributions of nest-site characteristics for Tree Swallows, other species and unoccupied cavities. Scale values (X-axis) represent midpoint values for each class.

TABLE 1. Nest-site characteristics for Tree Swallows, unoccupied nest sites, and other species at Allan's Pond and Osprey Marsh.

Character	Tree Swallows (n = 48) $\bar{x}$ ± SE	Unoccupied (n = 19) $\bar{x}$ ± SE	Other species (n = 20) $\bar{x}$ ± SE
Snag height (m)	4.3 ± 0.3	5.4 ± 0.5	5.9 ± 0.4
Cavity height (m)	3.4 ± 0.3	4.2 ± 0.4	4.0 ± 0.3
Snag girth at base (cm)*	83.2 ± 3.5**	85.4 ± 5.0	97.0 ± 3.6**
Snag girth at cavity (cm)*	69.8 ± 2.6**	74.3 ± 4.7	82.9 ± 3.5**
Entrance height (cm)	7.6 ± 0.7	7.0 ± 0.5	8.3 ± 1.0
Entrance width (cm)*	5.3 ± 0.3**	5.6 ± 0.3	6.0 ± 0.3**
Entrance area (cm^2)	32.4 ± 3.8	32.1 ± 3.7	39.8 ± 5.0
Cavity volume (cm^3)*	1,251.8 ± 162**	2,025.0 ± 389	2,483.7 ± 344**

* Kruskal-Wallis test, frequency distributions of three nest-site classes are significantly different, $P < 0.05$.
** GT2 pairwise comparison, indicated means are significantly different, $P < 0.05$.

means in Table 1, $n = 48$). Cavities were located in snags that ranged from <2 m to >9 m in height, although most (75%) were in snags <6 m tall, and a substantial proportion (27%) were in stumps of fallen trees which were <2 m tall. Almost half (46%) of the cavities used were located less than 2 m above the pond surface. Tree Swallows used cavities >6 m above the pond surface infrequently, but also occupied the two highest cavities available in both study sites (8.3 m, >9.0 m).

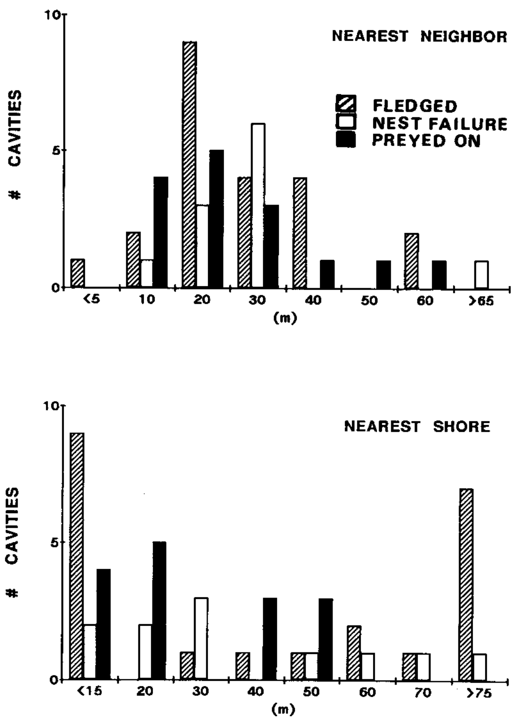

FIGURE 2. Frequency distributions of nest spacing by Tree Swallows for successful nests, failed nests, and nests that suffered predation.

Circumference at the base of the snag ranged from <50 cm to >130 cm, but most nests were in snags with a girth of 60–90 cm. Girth at the cavity entrance ranged from 41 cm to 105 cm, with nests distributed evenly throughout this range.

Cavity-entrance heights were extremely variable, ranging from 3.5 cm to 26 cm. Six cavities had very large entrance heights (>11 cm). Entrance width, which ranged from 2 to 16 cm, was not as variable as entrance height. Almost half of all entrance widths were between 4.0 and 5.0 cm.

The entrance area for Tree Swallow cavities ranged from 11.3 to 326.7 cm^2, with most (75%) below 35 cm^2. It appeared that decay produced both the entrances and cavities of the largest nests.

Cavity volume had a particularly broad range (219–6,370 cm^3). Most Tree Swallow cavities (60%) were less than 1,000 cm^3.

Mean distance from a nesting pair of Tree Swallows to its nearest conspecific neighbor was 27.1 m (SE = 2.1, Fig. 2). Sixty-two percent of Tree Swallow pairs nested between 15 and 35 m from the nearest conspecific pair. A few pairs nested over 45 m from the nearest conspecifics, while two pairs nested within 3.6 m of each other. Nearest-neighbor analysis (Clark and Evans 1954) revealed that breeding pairs at AP in 1986 (R = 1.406, $P \ll 0.0001$), and at OM in 1986 (R = 1.268, $P = 0.02$) and 1987 (R = 1.252, $P = 0.04$), nested further away from one another than expected. Pairs at AP in 1987 tended to be uniformly spaced, but not significantly.

Mean distance to shore of a pond for nest sites of Tree Swallows was 38.8 m (SE = 5.0, Fig. 2).

Tree Swallow nest sites were typically within 55 m of the shore of both ponds (77%). OM, however, is much larger than AP, allowing some pairs to nest as far as 128 m from the shore.

Other species. Many other secondary cavity-nesting species were present in both study sites including European Starlings, Common Grackles (*Quiscalus quiscula*), Eastern Bluebirds (*Sialia sialis*), Northern Flickers (*Colaptes auratus*), and Great Crested Flycatchers (*Myiarchus crinitis*). For both sites combined, starlings occupied a total of 29 cavities and 39 cavities in 1986 and 1987, respectively. Grackles occupied five and 16 cavities, respectively, in 1986 and 1987. Flickers nested in two cavities at AP in 1986 and 1987, Eastern Bluebirds nested in one cavity at both AP and OM in 1986, and Great Crested Flycatchers occupied three cavities at AP in 1987.

Means of characteristics for nest sites of other species were all greater than those for Tree Swallows (Table 1, Fig. 1). Girth of the snag at the base (Kruskal-Wallis one-way ANOVA, $H = 6.32$, df = 2, $P = 0.04$) and at the cavity ($H = 6.51$, df = 2, $P = 0.04$), entrance width ($H = 6.94$, df = 2, $P = 0.03$), and cavity volume ($H = 13.03$, df = 2, $P = 0.002$) had significantly different medians between nest sites for Tree Swallows, other species, and unoccupied nest sites. A posteriori pairwise comparisons (Hochberg's GT2 method, Sokal and Rohlf 1981) on the ranks of the means of these four variables showed Tree Swallow nest sites differed significantly from the nest sites of other species (Table 1). Therefore, other species generally nested in thicker snags, and occupied nest sites with larger entrance widths and larger volumes.

REPRODUCTIVE SUCCESS

Mean clutch size for Tree Swallows was 4.68 (SE = 0.15, $n = 25$). Due to a small sample size, all clutches were considered together despite evidence of possible differences in clutch sizes between different age classes of females (DeSteven 1980, Stutchbury and Robertson 1988). Linear regression analyses were performed to examine whether cavity volume and floor area influenced clutch size. Values for cavity volume and floor area were first transformed using natural logarithms. The regressions showed that floor area ($F = 3.48$, df = 23, $P = 0.05$, $R^2 = 0.13$) significantly influenced clutch size of breeding females, while cavity volume ($F = 1.23$, df = 23, $P = 0.31$, $R^2 = 0.05$) did not.

Fifteen of 48 (31%) Tree Swallow nests were preyed on (Fig. 3), likely by raccoons, *Procyon lotor*, or possibly by flickers (Rendell and Robertson, unpubl. data). In 13 of those 15 events the nest cavity was destroyed. Such cavities were torn open exposing the entire inside of the cavity. No cavities depredated in 1986 were subsequently used by Tree Swallows in 1987. Eleven of 48 (23%) nests failed for other reasons (e.g., abandoned, nestling death). Median snag height (Kruskal-Wallis one-way ANOVA, $H = 10.87$, df = 2, $P = 0.004$) and cavity height ($H = 13.92$, df = 2, $P = 0.0009$) were significantly different between successful nests (22/48 = 46%), failed nests and nests that were depredated (Table 2). A posteriori pairwise comparisons showed nest sites where young fledged were significantly higher than those which were preyed on (Table 2). In particular, nest sites <4 m in height from the pond surface were depredated with greater frequency. In other respects, nest-site characters were similar for successful nest sites, failed nest sites and those that were preyed on (Table 2, Fig. 3).

Distance to nearest neighbor was very similar for the three groups of Tree Swallow pairs and did not influence breeding success (Table 2, Fig. 3). The mean distance to nearest shore for nest sites where young fledged was considerably greater than for the other classes (Table 2), however, the medians were not statistically significant (Kruskal-Wallis one-way ANOVA, $H = 1.07$, df = 2, $P = 0.59$).

Principal component analysis was used to portray the general trends in characteristics of nest sites that influence reproductive success. Our interpretation of the analysis follows the approach of Conner and Adkisson (1977). Three principal components (PC) explained 66.4% of the total variance (Table 3). For PC1 high correlations with characteristics correspond to higher nest cavities with large entrances, away from shore, while low correlations represent short, shoreline snags with lower cavities. High values of PC2 correspond to short, thick snags close to other breeding pairs, and therefore represent a continuum from more solitary, taller, thinner snags to clumped, shorter snags. Finally, increasing values of PC3 represent a trend from shorter snags with relatively large cavities to taller snags with relatively small cavities.

Nest sites that fledged young show high values for PCs 1 and 3 where tall snags and high cavities are typical (Fig. 4; nest sites whose outcome was

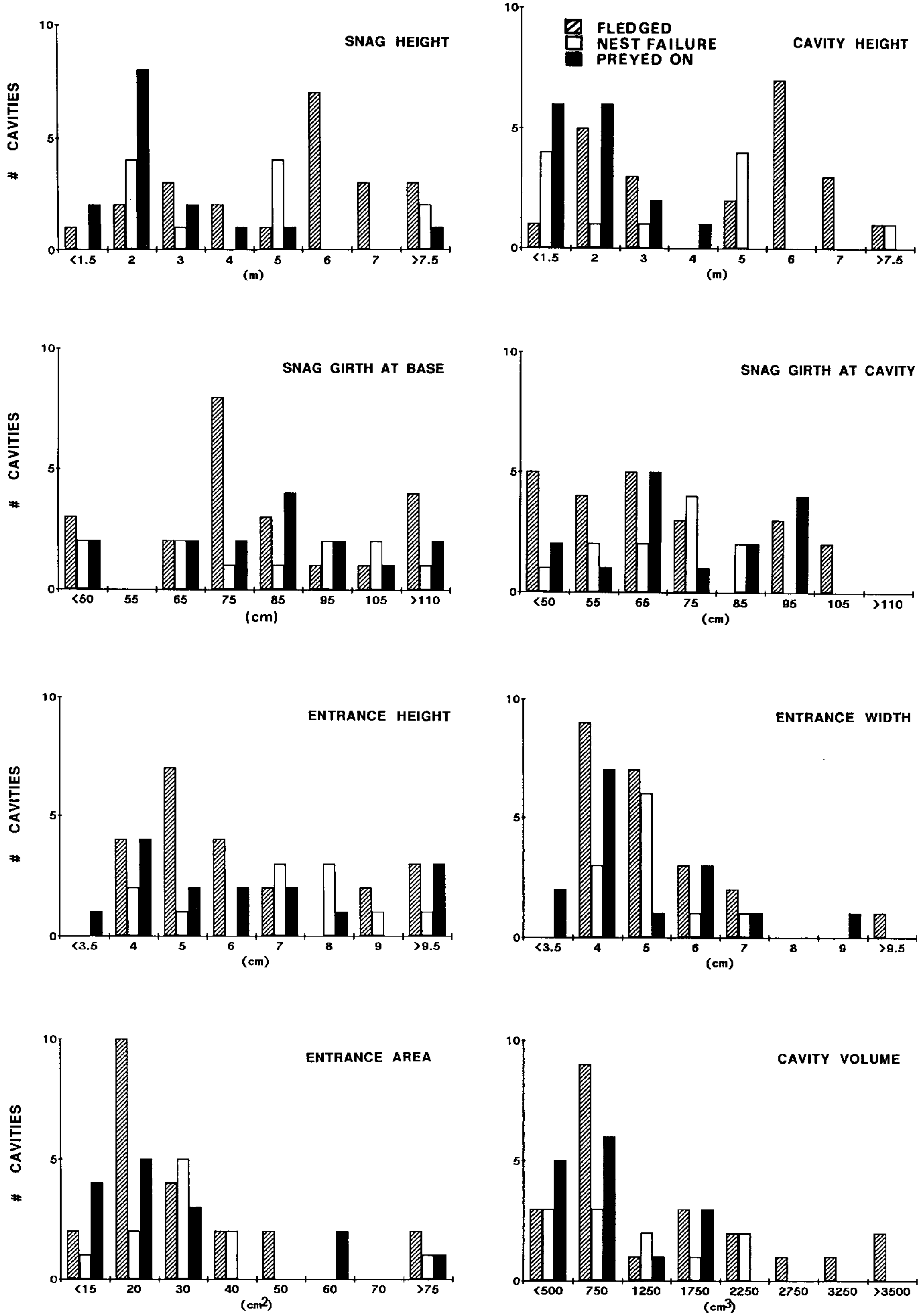

FIGURE 3. Frequency distributions of nest-site characteristics of Tree Swallows for successful nests, failed nests, and nests that suffered predation.

TABLE 2. Nest-site characteristics of Tree Swallows for successful, failed (abandoned, nestling death), and depredated nests at Allan's Pond and Osprey Marsh.

Character	Fledged (n = 22) $\bar{x}$ ± SE	Nest failure (n = 11) $\bar{x}$ ± SE	Preyed on (n = 15) $\bar{x}$ ± SE
Snag height (m)*	5.2 ± 0.4**	4.7 ± 1.0	2.8 ± 0.2**
Cavity height (m)*	4.5 ± 0.5**	3.4 ± 0.7	1.8 ± 0.2**
Snag girth at base (cm)	82.4 ± 4.7	82.9 ± 8.0	84.7 ± 6.6
Snag girth at cavity (cm)	68.0 ± 4.4	67.8 ± 3.5	73.7 ± 4.7
Entrance height (cm)	7.7 ± 1.2	8.2 ± 1.5	7.0 ± 1.0
Entrance width (cm)	5.6 ± 0.5	5.0 ± 0.3	5.0 ± 0.4
Entrance area (cm^2)	32.7 ± 5.6	32.3 ± 5.6	31.9 ± 8.2
Cavity volume (cm^3)	1,571.4 ± 316	1,193.9 ± 219	825.1 ± 113
Nearest neighbor (m)	27.9 ± 3.1	27.6 ± 4.2	25.5 ± 3.8
Nearest shore (m)	47.9 ± 9.2	37.5 ± 8.6	26.4 ± 4.5

* Kruskal-Wallis test, frequency distributions of three nest-site classes are significantly different, $P < 0.05$.
** GT2 pairwise comparison, indicated means are significantly different, $P < 0.05$.

abandonment or nestling mortality [n = 11] were removed to reduce clutter). Also, cavities that fledged young show negative values for PC2, tending to be taller, thinner, solitary snags. Nests that were preyed on have positive values for PC2 and lower values for PC1, showing that shorter, clumped snags and those closer to shore, were preyed on more. This description generally supports our previous results. Cavity height was the main characteristic defining subsequent breeding success, but elements of cavity size and proximity to shore may also influence reproductive success for Tree Swallows in these populations.

TABLE 3. Results of principal component analysis on nest-site characteristics of breeding Tree Swallows (n = 48). Characteristics are: snag height, SNH; cavity height, CVH; snag girth at the base, SGB; snag girth at the cavity, SGC; entrance height, ENH; entrance width, ENW; entrance area, ENA; cavity volume, CVV; nearest neighbor, NRN; and nearest shore, NRS.

	Principal component		
	I	II	III
Percentage total variance	30.6	22.0	13.8
Cumulative percentage of total	30.6	52.6	66.4
Correlations of components to nest-site variables			
SNH	0.45	−0.25	0.44
CVH	0.41	−0.37	0.41
SGB	0.19	0.55	0.39
SGC	0.13	0.62	0.12
ENH	0.40	0.04	−0.43
ENW	0.46	−0.10	−0.39
CVV	0.20	0.10	−0.35
NRN	−0.22	−0.26	−0.01
NRS	0.34	0.10	−0.09

NEST-SITE AVAILABILITY

Surveys conducted in 1986 of all snags in AP and OM together found 178 available cavities (AP n = 96, OM n = 82), of which 100 were occupied and/or defended by either Tree Swallows (n = 62; 52 cavities used and 10 not used but involved in multiple defenses) or other species (n = 38). Thus, 78 cavities (78/178 = 44%; n = 39 each for both AP and OM) were available, but not used.

Unused nest sites had mean snag height, girth at base and cavity, entrance width, and cavity volume that fell between nest sites used by Tree Swallows and those used by other species, but were not significantly different from either group (Table 1). Mean entrance height and area of unused sites were lower than those used by either Tree Swallows or other species. However, since individual pairs of Tree Swallows occupied cavities with entrance height and area well below this mean, entrance size per se was not prevent-

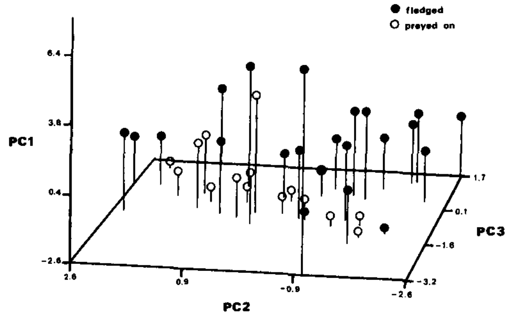

FIGURE 4. Three-dimensional diagram of successful and depredated nest sites of Tree Swallows (n = 37). The diagram is plotted using the first three principal component scores for each snag.

ing occupancy by Tree Swallows. Unused sites were slightly higher, on average, than those used by either Tree Swallows or other species.

The dispersion of 18 of the 19 unoccupied cavities relative to the closest, active Tree Swallow nest sites during 1986 were measured in 1989 (1/19 unoccupied snags fell since 1987). Four of 18 unoccupied cavities were included in 'multiple nest defenses' by Tree Swallows (see Discussion). Of the remaining 14 sites, mean inter-nest distance between unoccupied cavities and Tree Swallow cavities was 24.2 m (SE = 2.2; range = 5.1–35.0 m).

Three factors, including predation (13 snags destroyed, see above), affected the total number of nest sites available for use in our populations. Decay caused seven snags with previously occupied cavities to fall down in storms (four in 1986, three in 1987). Also, over 2 years woodpeckers excavated only five new cavities in our study sites, three of which were used by Tree Swallows during the study. Considering the effects of all three factors together, there was a net loss of 9% (20 − 3 = 17, 17/178) of available cavities in our sites over 2 years.

DISCUSSION

NEST-SITE CHARACTERISTICS

We found considerable variability in characteristics of nest sites used by Tree Swallows. Tree Swallows occupied the lowest cavities, and those with the smallest entrances and volumes, but also used the highest cavities, and those with the largest entrances and volumes. Similarly, Munro and Rounds (1985) found that Tree Swallows showed the greatest variability in characteristics of occupied nest boxes compared with four other passerine species in Manitoba. However, Lumsden (1986) showed Tree Swallows, when given a choice, did exhibit a preference for certain nest boxes (e.g., with larger volumes, 4,588 cm^3 vs. 1,935 cm^3). Tree Swallows in our study should prefer higher cavities with larger volumes to enhance reproductive success (see Reproductive Success below); however, our results of nest-site use contradict this post hoc prediction. Tree Swallows may have chosen shorter, smaller cavities, perhaps to avoid nest usurpation by interspecific competitors (see below).

Tree Swallow nest sites were uniformly dispersed in the study areas, suggesting that pairs spaced themselves according to the proximity of the nearest conspecific. In nest-box experiments, Muldal et al. (1985) showed that, within a radius of 36 m, Tree Swallows preferred to nest as far as possible from conspecifics. This spacing, achieved through territorial defense of the area around the nest site, as well as mutual avoidance, may reduce the threat of nest usurpation (Robertson and Gibbs 1982, Leffelaar and Robertson 1985) and of cuckoldry (Lombardo 1986). On the other hand, the spacing pattern of Tree Swallows in natural habitats may result at least in part from the spatial dispersion of cavities, and not from an active process of nest-site selection.

Comparison of our results with other studies should be done with caution because of differences among study sites. Most natural cavity studies are conducted in terrestrial habitats, sometimes only including cavities in living trees. Our sites are old (ca. 50–75 years) beaver ponds where decay and snag fall result in many short stumps throughout the ponds. This accounts for the large number of low cavities available to Tree Swallows. Many characteristics frequently considered when examining cavity nest-site occupation (e.g., canopy height, Peterson and Gauthier 1985; tree species diversity, Swallow et al. 1986) are not applicable to our study. Snags in our sites lack limbs or crowns and the species of trees are difficult to identify. Finally, the presence of many breeding hole-nesters in a relatively small beaver pond allows for an assessment of population and community interactions that may not be possible in other studies.

REPRODUCTIVE SUCCESS

Reproductive success of Tree Swallows was influenced by two nest-site characteristics: cavity height (cf. Nilsson 1984a) and cavity floor area (cf. Ludescher 1973). Higher cavities suffered less predation than lower ones, probably due to accessibility. Raccoons, the main predators at our sites, likely could not climb to higher nests because of these animals' large size and extremely poor snag condition.

Tree Swallow clutch sizes were positively influenced by cavity floor area in our natural nest sites, but not by cavity volume. Significantly larger clutches found in nearby nest-box populations (Robertson and Rendell, in press), where cavity volume and floor area are greater, show that floor area and/or cavity volume definitely influence clutch size in Tree Swallows (for other species in natural holes cf. Ludescher 1973, Nilsson 1984b, but also Alatalo et al. 1988).

Although the location of a nest in relation to other nests or the shore might be expected to influence reproductive success (through conspecific interference and the threat of predation, respectively), neither measure of spatial distribution had any significant effect. However, nest sites where predation occurred were much closer to shore than those where young fledged ($\bar{x} = 26$ m vs. 48 m), suggesting that proximity to shore facilitates detection of active nests by mammalian predators. Principal component analysis generally supports this observation.

NEST-SITE AVAILABILITY

Interspecific (cf. Weitzel 1988) and intraspecific (Robertson and Gibbs 1982, Leffelaar and Robertson 1985) conflicts for nest sites, floating populations of sexually mature individuals without nest sites (Stutchbury and Robertson 1985), the rapid occupation of artificial nest sites (Holroyd 1975), rapid replacement of breeding individuals in removal studies (Robertson and Stutchbury 1988), and higher breeding densities with the provision of nest boxes (Brawn and Balda 1988) are all interpreted as the result of limited nest-site availability for secondary cavity-nesting birds. However, recent studies have documented the presence of unoccupied cavities in the vicinity of breeding hole-nesters (e.g., 54–93% occupancy of available holes, van Balen et al. 1982; cf. Ingold and Ingold 1984, Peterson and Gauthier 1985, McCallum and Gehlbach 1988), apparently contradicting the theory of nest-site limitation. Some studies found differences between occupied and unoccupied nest sites (van Balen et al. 1982, McCallum and Gehlbach 1988), but neither our study nor that of Ingold and Ingold (1984) found differences between the two cavity types. Unoccupied cavities were, therefore, apparently suitable for use as nest sites, and so cavities themselves were not strictly limiting in our populations.

Despite the indication that nest sites are available for use in our populations, certain factors do influence nest-site availability. First, nest-site destruction by predators, snag fall, and infrequent excavation of new cavities by woodpeckers showed that our sites are losing 9% of available nest sites every 2 years.

Second, other species occupied many of the larger cavities in our populations, limiting nest-site availability by occupancy and/or aggressive interactions. Our results suggest entrance size and cavity volume may limit access to many cavities for those species with larger body size, leaving smaller cavities available for Tree Swallows. Tree Swallows, however, are plastic in their choice of cavities, so fewer pairs of other species may allow more Tree Swallows to breed. Aggressive conflicts over nest sites were common. For example, Tree Swallows apparently lost two nest sites with clutches to excavating flickers in 1986 (but usurped two nest sites from excavating flickers in 1987; Rendell and Robertson, unpubl. data). In these two instances of apparent predation by flickers, completed clutches of Tree Swallows disappeared from cavities coinciding (within 48 hr) with enlargement and use of these same cavities by flickers. Whether or not the eggs were consumed by flickers or simply ejected from the cavities is not known. Some unused nest sites may have been avoided by Tree Swallows due to the threat of usurpation by other species. Several characteristics (e.g., entrance width, cavity volume) of unoccupied cavities were intermediate to those of nest sites for Tree Swallows and other species, and so may have been more vulnerable to takeover. In nearby grids of nest boxes, Tree Swallows usually avoid nest sites near hedgerows where House Wrens (*Troglodytes aedon*) subsequently nest (Robertson, unpubl. data), indicating that birds may incorporate the likelihood of interference from other species in their decision regarding choice of nest site. We do not have information regarding territory size for other cavity nesters in our sites, nor for temporal changes in cavity availability. With several unoccupied cavities in our sites, data on temporal availability seems irrelevant.

Third, territorial defense by conspecifics of more than one nest site limited access to cavities for Tree Swallows (Rendell 1987). These 'multiple nest defenses' may include defense by residents of one or two extra nearby cavities from conspecifics and other species. Four of 18 unoccupied nest sites were included in known multiple nest defenses. Further, Tree Swallows breeding in nest-box grids, where nest sites were arranged in rows and columns throughout hay fields, were observed to defend extra nest boxes at distances of 28 to 40 m from a focal box (Stutchbury and Robertson 1987b). Fourteen of 18 unused nest sites in our study were all within 35 m of cavities of breeding Tree Swallows. This suggests that, although the remaining 14 unused nest sites were not observed to be involved in multiple nest defenses, Tree Swallow pairs may have included these unoccupied sites in their territories, thereby preventing conspecifics from using them.

Why were some cavities unused when floating populations are present locally (Stutchbury and Robertson 1985)? It is possible that Tree Swallows avoided cavities with characteristics similar to those used by interspecific competitors due to the greater threat of usurpation, but it appears more likely that intraspecific territoriality, and more specifically defense of more than one cavity by breeding pairs, was responsible for the large proportion of unoccupied nest sites in our populations.

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