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DO TREE SWALLOWS USE NEST CAVITIES AS NIGHT ROOSTS DURING TERRITORY ESTABLISHMENT?

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Abstract.—Nest cavities of Tree Swallows (*Tachycineta bicolor*) were examined at dawn during the period of territorial establishment to determine if Tree Swallows regularly roost in their cavity. We discovered communal roosts on only 2 of 9 mornings in April 1985, and 0 of 15 mornings in April 1986. A total of 73 birds were found in communal roosts, with one nest cavity containing 25 birds, and 4–16 birds in 5 other cavities. A total of 14 birds were found roosting with one other bird, and 18 birds roosting alone. Only a small proportion (0–10%) of the resident birds roosted singly or with one other bird in their nest cavity on a given night, and this was not correlated with air temperature at dawn or at sunset the night before. Communal roosting is likely a response to severe energetic stress, whereas roosting alone or with one other bird may play some role in territorial establishment for the small proportion of birds exhibiting such behavior.

¿USA *TACHYCINETA BICOLOR* CAVIDADES DE ANIDAR, PARA PERNOCTAR, DURANTE EL PERÍODO DE ESTABLECIMIENTO DEL TERRITORIO?

Sinopsis.—Fueron examinadas al amanecer, cavidades de anidamiento utilizadas por golondrinas (*Tachycineta bicolor*) durante el período en que estas aves establecen su territorio, para determinar si los pájaros pernoctaban en las cavidades. Durante el mes de abril de 1985 y 1986, descubrimos pernoctación comunal en 2 de 9 y 0 de 15 mañanas de búsqueda. Un total de 73 golondrinas fueron encontradas pernoctando comunalmente con una cavidad conteniendo 25 aves y otras cinco cavidades conteniendo de 4–16 individuos. Catorce aves fueron encontradas pernoctando con otro individuo y 18 de forma individual. Tan solo una pequeña proporción de las aves residentes (0–10%) pernoctaron individualmente o con otro individuo en una noche particular. Esto no estuvo correlacionado con las temperaturas crepusculares o del amanecer. El pernoctar en grupos parece ser una respuesta a la tensión energética causada por bajas temperaturas y reducidas reservas energéticas corporales, mientras que el pernoctar solo o con otra ave podría tener alguna función en el establecimiento del territorio de anidamiento.

This study examines the early spring roosting behavior of a cavity-nesting species, the Tree Swallow (*Tachycineta bicolor*). Tree Swallows have been found dead and alive in cavities in groups (Chapman 1955, Christy 1940, Dence 1946, Stake and Stake 1983, Weatherhead et al. 1985) or alone (R. Cohen, pers. comm.; Lombardo 1986) after cold weather, which suggests that cavity-roosting may be an important component of their behavior early in the spring. In this study we examined the frequency with which Tree Swallows roosted in their nest cavities early in the spring, and consider whether this behavior is related to thermoregulatory advantages or nest site defense.

Night is critical for small birds faced with surviving cold spring weather,

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since temperatures are usually lowest and birds generally cannot feed during this time. Many species roost in groups and form tight clusters (e.g., Beal 1978, Grubb 1973, McNicholl 1979, Meservey and Kraus 1976, Smith 1972), a behavior which has been shown to conserve energy in some species (e.g., Buttemer 1985, Kelty and Lustick 1977, O'Connor 1978). Cavity-nesting birds may gain an additional thermoregulatory advantage by roosting inside tree cavities (e.g., Brown 1976; Buttemer et al. 1987; Chaplin 1982; Frazier and Nolan 1959; Kendeigh 1961; Knorr 1957; Lombardo et al., in press; Mayer et al. 1982).

Cavity-nesting species may roost also in cavities overnight as a means of defending the nest site (Lombardo et al., in press). In the Purple Martin (*Progne subis*), a secondary cavity-nester, males and females roost overnight in their cavity beginning from the first day that they establish a territory in the colony (Brown 1980). Our study examines whether the Tree Swallow, also a secondary cavity-nester, roosts overnight in its nest cavity as a component of nest site establishment and defense.

METHODS

This study was conducted at the Queen's University Biological Station, Chaffey's Lock, 50 km north of Kingston, Ontario. The Tree Swallow population studied breeds in nest boxes distributed throughout four hay-fields that cover about 5 ha. This population was established in 1976, and has had 55–65 breeding pairs since 1982. In this area, Tree Swallows begin arriving in late March, and by mid-April most of the nest sites are defended by a pair (Stutchbury and Robertson 1987a). We considered the resident population to consist of those individuals that bred in nest boxes in our study area in a given year, plus those individuals that remained in the area but did not breed (i.e., floaters; Stutchbury and Robertson 1985). There were 53 nest boxes evenly spaced in the four main fields in 1985, and 74 in 1986. All boxes were the same size (15 × 17 × 31 cm) and mounted on aluminum posts about 1.5 m high.

This study began in 1985, when we discovered a group of birds roosting in a nest box early in the morning of 9 Apr. We subsequently checked all 53 nest boxes between 0600 and 0700 EST on five of the next nine mornings when overnight temperatures were at or below freezing. In 1986, we systematically checked all 56 boxes in the two largest fields beginning around 0500 EST, before sunrise (about 0530 EST), on 15 of 16 mornings between 3–18 Apr. This is the critical period for territory establishment, since all resident birds that settled in these nest sites in April 1986 obtained their territories by 18 Apr. Just before sunrise, we commonly observed the first Tree Swallows circling high above the fields, and slowly descending during about 10 min to perch on their nest sites. In a subsequent study at this site, boxes which were checked after dark and found to have communal roosts still had roosting birds at dawn the next morning, and no additional roosts had formed in boxes found vacant at night (Robertson, unpubl. data). Therefore, we are confident that birds found in their boxes at dawn had spent the night there.

Birds were easily captured when they were inside a nest box, and there were few instances where a bird flew out as we approached the box. Each bird caught was banded with a Canadian Wildlife Service numbered band, weighed with a 50 g pesola spring balance, and the maximum flattened wing length and the extent of brown plumage on the forehead were measured to the nearest millimeter. Adults caught inside boxes were sexed on the basis of past banding data, brown as opposed to iridescent blue-green plumage (Hussell 1983), the presence or absence of brown plumage on the forehead, wing length (Stutchbury and Robertson 1987b), or the subsequent development of a brood patch or cloacal protuberance.

Daily air temperatures in Kingston during April were obtained from the Kingston Weather Office, operated by Environment Canada.

RESULTS AND DISCUSSION

There were only two mornings on which we found more than two birds roosting in a single cavity (i.e., communal roosting). On 9 Apr. 1985 there were four birds roosting in one cavity, and on 11 Apr. 1985 we found 5, 6, 16, 17, and 25 birds roosting in five different cavities located in three of the fields. Half of the birds found roosting communally were of unknown sex, and the sex ratio of the remaining birds did not differ significantly from 1:1 (Table 1; Binomial test, $P = 0.43$). Only 16% (11/69) of the birds were subsequently residents in the study area that year. At the time these roosts were found, we estimate that about 20 pairs were defending nest sites in our study area, based on the settlement pattern in this population in 1986 (Stutchbury and Robertson 1987a). Therefore the 11 residents found roosting communally represented about 25% of the residents that were likely present at that time.

The proportion of roosting birds that subsequently bred in the population may have been lowered due to the disturbance of being captured inside nest cavities. Females captured in their nest cavities before the late incubation stage are more likely to abandon their nests than females captured later in the breeding season (Burtt and Tuttle 1983, Lombardo 1989). However, only 11% of the 69 birds roosting communally had bred previously in this population, compared with the typical 50–60% in the breeding population. This suggests that many of the birds in the communal roosts were passing through the area on migration, and did not necessarily leave the area due to their capture. Furthermore, for birds roosting alone or with one other bird, 64–72% (Table 1) remained as residents, indicating that handling per se was not the sole cause of the low level of residency among the communally roosting birds.

In contrast to the nightly communal roosts formed in some wintering populations of cavity-nesters (Buttemer et al. 1987; Pitts 1976; Sydeman and Guntert 1983; but see Lombardo et al., in press), we found no communal roosts during our regular nest checks in 1986. These results suggest that resident Tree Swallows do not regularly roost communally in their nest cavities early in the breeding season.

Since communal roosting has a potentially high risk of mortality due

TABLE 1. The sex (M = male, F = female, and U = unknown) and residency status of birds found roosting communally (more than 2 birds), with one other bird, or alone in nest boxes in April 1985 and 1986 (n = number of birds). Recaptures of the same individual within a year were excluded.

	Number of birds	Sex			Residents that year	Bred in that box
		M	F[b]	U		
Communal	69[a]	16	18	35	11 (16%)	0
One other	14	5	6	3	9 (64%)	5 (36%)
Alone	18	3	13	2	13 (72%)	7 (38%)

[a] An additional four birds were not banded or sexed.
[b] All females were after-second-year.

to being trapped under other individuals (Weatherhead et al. 1985), birds are expected to roost communally only when they are sufficiently energetically stressed that the benefits of heat conservation outweigh the risks of roosting in large groups. Such energetic stress can be the result of very cold temperatures, and reduced body reserves.

The day on which several communal roosts were found (11 Apr. 1985) followed four days on which the minimum daily temperature was below freezing (Fig. 1). Although similar daily temperatures occurred on several other days in 1985 and 1986 (Fig. 1), there was no other period of four consecutive days of very low temperatures. A single day of cold temperatures may not represent a severe enough condition to favor communal roosting. However, sustained periods of cold temperatures that are accompanied by a reduced activity of flying insects would likely decrease the energy reserves of aerial insectivores, such as the Tree Swallow (Stocek 1986). The birds caught on 9 and 11 Apr. 1985 had a significantly smaller body mass than birds caught before 0800 on other days in April that year (Fig. 2; ANOVA: $F = 41.06$, df = 8, $P < 0.0001$). This pattern is not due to a biased sex ratio among communal roosters (Table 1). Furthermore, based on a sample from April 1987, males only average 1 g heavier than females during the pre-egg-laying period (males: $\bar{x} = 21.7$ g, SD = 1.8, $n = 23$, range = 17.5–24; females: $\bar{x} = 20.7$ g, SD = 1.3, $n = 36$, range = 18–23), which is not enough to account for the 3–4 g difference between birds caught on the days of communal roosting and those caught later in April.

Interestingly, the mean body mass of birds roosting communally was about 18 g, which is intermediate between the mass of Tree Swallows found dead after cold weather (14–15 g; Weatherhead et al. 1985, Whitmore et al. 1977), and Tree Swallows caught on other days in April 1985 or 1986 (20–23 g; Fig. 2). Although not conclusive, these results suggest that both unusually low air temperatures and low body mass are important factors that favor communal roosting in Tree Swallows.

Apart from the few cases of more than two birds roosting together, all other birds found roosting in cavities in April 1985 and 1986 were alone

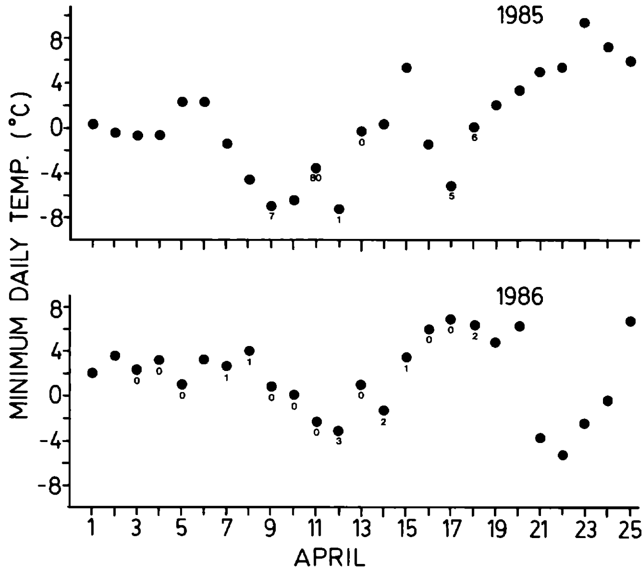

FIGURE 1. Minimum daily temperature in April 1985 and 1986. The total number of birds found in all boxes on days that box checks were conducted is shown below each point.

or with one other bird. Over both years, there were seven cases where we caught two birds in one cavity (Table 1). In two of these cases one of the pair was of unknown sex. Although three cases involved a male and a female, two cases involved birds of the same sex (in one case males, and the other females). Therefore, roosting with one other bird may not simply represent nest defense by a mated pair, as occurs in the Purple Martin (Brown 1980). Even if some of these birds abandoned their nests due to capture, most (64%) were residents that year in our study population, and many of them bred in the box in which they were captured.

Of the 16 individuals of known sex we found alone in a box, the sex ratio was strongly biased toward females (Table 1; Binomial test, $P = 0.011$). Most of the lone birds were residents, and many of those residents bred in the cavity in which they were found roosting. There were no unmated females defending nest sites during this period, indicating that females are more likely to use their nest cavities for roosting than males.

In 1986, the number of pairs defending a nest site rose gradually from 12 pairs on 3 Apr. to 35 pairs by 18 Apr. Despite the large number of birds established in the resident population, only 0–10% of them ever roosted in their cavities on a given night (Fig. 1). Not only were a small number of residents involved, but in 1986 only two of the eight residents that roosted in a cavity were found roosting on a second occasion.

One or two birds in a cavity would not gain as much advantage in terms of conserving heat as they would by huddling in large numbers,

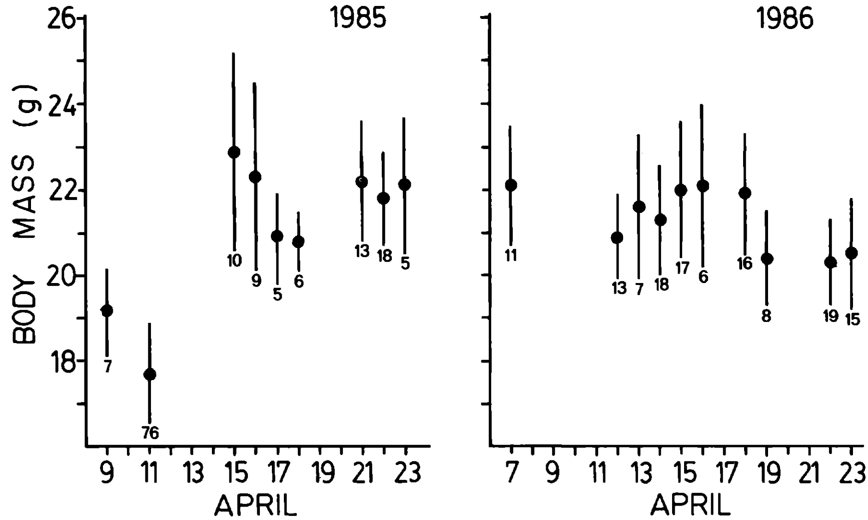

FIGURE 2. The mean body mass of all birds caught before 0800 in April 1985 and 1986. Bars are standard deviations, and numbers represent sample sizes.

but even one or two birds in a cavity can significantly reduce the energy expenditure of roosting birds (Buttemer et al. 1987, Chaplin 1982, Kendeigh 1961, Mayer et al. 1982, O'Connor 1978). However, the total number of birds found roosting alone or with one other bird in 1986 was not significantly correlated with minimum daily temperature (Fig. 1; $r_s = -0.05$, $n = 15$, $P > 0.05$), or with temperature at sunset the previous night ($r_s = 0.03$, $n = 15$, $P > 0.05$). Unlike communal roosts, on some occasions birds were found roosting alone or with one other bird after relatively warm nights. The body weights of birds roosting alone or with one other bird in April 1986 ($\bar{x} = 20.9$ g, SD = 1.1, $n = 8$; excluding recaptures) were similar to the weights of birds caught at other times in April that year (Fig. 2). Therefore, this behavior may not simply be a response to severe energetic stress.

Although only a small proportion of residents roosted in their cavities early in the spring, this behavior may play some role in territory establishment and defense. Both Purple Martins and Tree Swallows are secondary cavity nesters that arrive at their respective breeding grounds many weeks before the initiation of nest building and egg-laying. However, only the Purple Martin roosts regularly in its nest cavity during the territory establishment period. This suggests there is a fundamental difference in the territory establishment and nest defense tactics of these two species which merits further investigation.

Despite the potential energetic benefits of roosting in cavities, few resident Tree Swallows used this tactic. The benefits of early arrival in the spring are clear, since there is intense intrasexual competition for nest cavities within both sexes (Stutchbury and Robertson 1985, 1987a), as well as competition with other species (Holroyd 1975). The costs and benefits of various tactics of surviving cold spring weather will be impossible to evaluate without information on the location and thermal properties of the roost sites that Tree Swallows are using in the spring.

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