NEST ARCHITECTURE AND REPRODUCTIVE PERFORMANCE IN TREE SWALLOWS (*TACHYCINETA BICOLOR*)

MICHAEL P. LOMBARDO[1]

*Museum of Zoology, Department of Biology, and Michigan Society of Fellows,
University of Michigan, Ann Arbor, Michigan 48109, USA*

ABSTRACT.—Nests are an important component of parental effort in birds. From 1988 to 1990, I compared the architecture of nests built by subadult and adult female Tree Swallows (*Tachycineta bicolor*) in boxes in southeastern Michigan in order to determine if there were age-related differences in nest architecture and if these differences were associated with age-related differences in reproductive performance. Nests built by Tree Swallows were composed of a mat of dry grasses and a nest cup lined with feathers. On average, nest material filled approximately 30% of a nest box. I observed few age-related differences in nest architecture. However, nests built by subadult females were significantly less well feathered than nests built by adult females, but feather score was not correlated with the production of nestlings or fledglings. There were age-related and within-season variations in reproductive performance associated with variations in nest architecture, especially later in the season. Among subadult females that bred later in the season (i.e. after the population median date of clutch initiation), those females that built larger nests (as indicated by total nest volume, depth of material beneath the nest cup, and percentage of nest box filled with material) hatched more eggs per clutch. In 1990, subadult females that bred later in the season and built larger nests (as indicated by depth of material beneath nest cup and percentage of nest box filled with material) produced significantly more hatchlings but significantly fewer fledglings. Among adult females that bred later in the season, those females that built nests that filled a larger percentage of the nest box hatched fewer eggs. Adult females with nests having larger cups produced significantly more fledglings, but those with cups crowded with nestlings (as indicated by a cup index [total egg volume/nest cup volume]) produced significantly fewer fledglings. In 1990, adult females that bred later in the season and built larger nests (as indicated by depth of nest material, total nest volume, percentage of nest box filled with material) and had more-crowded nest cups produced fewer hatchlings and fledged a significantly smaller proportion of hatchlings. These results suggest that nestling hyperthermia in well-insulated nests may affect the reproductive performance of Tree Swallows that breed late in the season. *Received 11 January 1993, accepted 1 July 1993.*

NESTS ARE an important component of parental effort in birds. Nests provide safety from predators, a container for eggs and nestlings, and a microenvironment for developing eggs and growing nestlings (Collias and Collias 1984). Various aspects of nest architecture have the potential to influence reproductive performance. For example, in some hole-nesting species that nest in boxes (e.g. flycatchers [*Ficedula* spp.] and tits [*Parus* spp.]), clutch size is positively correlated with the area of the nest-box floor (Karlsson and Nilsson 1979, van Balen 1984,

Gustafsson and Nilsson 1985, Slagsvold 1987; but see Alatalo et al. 1988). Likewise, Møller (1982) found that clutch size was positively correlated with nest volume in the open-nesting Barn Swallow (*Hirundo rustica*) in Denmark.

Nest location and the amount of nest insulation may influence reproductive performance by affecting the timing of breeding (O'Connor 1978) and the energetic costs of incubation (e.g. Calder 1971, 1973, Walsberg and King 1978, Skowron and Kern 1980). The amount and type of nest material and insulation may affect brood thermoenergetics (Mertens 1977a) and increase the risk of nestling hyperthermia (Mertens 1977b).

The populations of nest parasites that often adversely affect reproductive performance (Moss

and Camin 1970, Brown and Brown 1986) may be correlated with the choice of nest materials (cf. Clark 1991 and references therein), the tightness of the weave of nesting materials (Burtt et al. 1991), and the number of feathers lining the nest cup (Mason 1944; but see Møller 1987, Rogers et al. 1991). Nest-predation rates are often greater at nests located closer to the ground (Nilsson 1984, Rendell and Robertson 1989).

Nest building is influenced by "instinct" and practice (Dilger 1962, Sargent 1965, Collias and Collias 1984). The nests of experienced birds are often superior to those built by novices (e.g. Village Weaver, *Ploceus cucullatus;* Collias and Collias 1964). Therefore, determining the fitness consequences of individual and age-related differences in nest architecture are important to a complete understanding of the factors affecting individual differences in reproductive performance.

The various influences of nest-cavity dimensions (e.g. floor area, cavity volume, cavity height from ground) on reproductive performance, especially clutch size, have been studied in numerous hole-nesting species in both natural cavities and nest boxes (e.g. Karlsson and Nilsson 1979, Gustafsson and Nilsson 1985, Alatalo et al. 1988, Robertson and Rendell 1990). However, the architecture of the nest itself is often not considered as a variable affecting reproductive performance. This lack of consideration of nest architecture is perplexing because differences in the insulation of nests built inside of cavities should have an effect on the energetics of incubation (Calder 1971, 1973, Walsberg and King 1978, Skowron and Kern 1980), as well as brood thermoregulation (Mertens 1977a, b).

I investigated the influence of female age on nest architecture in Tree Swallows (*Tachycineta bicolor*) nesting in boxes. I compared the architecture of nests built by subadult females with those built by adult females and examined the association between nest architecture and reproductive performance. Robertson and Rendell (1990) discussed the differences in breeding ecology between Tree Swallows nesting in natural cavities and nest boxes.

Tree Swallows build nests made of a mat of dry grasses with a nest cup lined with feathers. Females do most of the nest building (Kuerzi 1941, Sheppard 1977), but males add most of the feathers that line the nest cup (Sheppard 1977, Cohen 1985). Sheppard (1977) described

the nests built by subadult females as rudimentary with poorly formed cups containing fewer feathers than the nests of adult females.

Both nest-cup volume and nest feathering may influence the evolution of the age-related differences in reproductive performance that have been observed in Tree Swallows (DeSteven 1978, 1980, Stutchbury and Robertson 1988) because both factors have thermoenergetic effects. For example, female Broad-tailed Hummingbirds (*Selasphorus platycerus*) that incubate eggs in deep cups expend 50% less energy than do females that incubate eggs in shallow cups (Calder 1973). Thus, differences between subadult and adult female Tree Swallows in nest-cup dimensions could influence the energetics of incubation, ultimately influencing the evolution of age-related patterns in clutch size; subadult females lay clutches that, on average, are one egg smaller than the clutches of adult females (DeSteven 1978, Stutchbury and Robertson 1988, Lombardo unpubl. data).

The insulative qualities of feathers are well known (Wainwright et al. 1976). Eggs in well-feathered nests cool slowly between bouts of incubation allowing incubating females to spend more time foraging (White and Kinney 1974). Therefore, incubating females with poorly insulated nests may suffer energetic stress during periods of low ambient temperatures (White and Kinney 1974). In contrast, a well-insulated nest increases the risk of hyperthermia to endothermic nestlings (Mertens 1977b). Therefore, nest builders must make a trade-off between their energetic costs of incubation and the risks of hyperthermia to their nestlings (Møller 1984). Thus, I predicted that Tree Swallow nests built early in season, when the chances of experiencing low ambient temperatures during incubation are greater, would be larger and have more feathers than nests built later in the season, when ambient temperatures are higher and the risk of hyperthermia is greater.

METHODS

From 1988 to 1990, I studied Tree Swallows nesting in boxes at the University of Michigan's Edwin S. George Reserve Biological Research Station (42°27′N, 84°00′W). The George Reserve is located 39 km northwest of Ann Arbor, Michigan. One hundred wooden nest boxes were mounted on metal posts erected in grids in old fields and along trails around ponds. All nest-box entrance holes faced south. I deterred nest predators (e.g. racoons, *Procyon lotor*) from destroying

Nests built by subadult females ($\underline{n}$ = 52)

Sector 1.	Sector 2.	Sector 3.
4	18	5
Sector 4.	Sector 5.	Sector 6.
2	18	3
Sector 7.	Sector 8.	Sector 9.
1	0	1

Nests built by adult females ($\underline{n}$ = 69)

Sector 1.	Sector 2.	Sector 3.
3	29	4
Sector 4.	Sector 5.	Sector 6.
1	31	1
Sector 7.	Sector 8.	Sector 9.
0	0	0

Fig. 1. Female age and nest-cup position in Tree Swallow nests. Nest-box floors were divided into nine sectors. Sector number indicated in upper-left-hand corner of each sector. Nest-box opening was above sector 8. Values indicate number of nests with center of nest cup located in particular sectors.

nests by applying axle grease to nest poles before each season.

Breeding female Tree Swallows were categorized as either adult or subadult based on plumage characteristics (Hussell 1983). Females in mostly brown dorsal plumage are second-year birds (SY) and were classified as subadults, whereas females in mostly iridescent blue-green dorsal plumage are after-second-year birds (ASY) and were classified as adults. Some females were intermediate in plumage and were conservatively classified as subadults (Hussell 1983). Males develop the monomorphic full adult breeding plumage before their first winter (Dwight 1900).

Breeding females were captured on their nests between 0600 and 0800 EST on the seventh day after clutch completion. Tree Swallow females begin to incubate eggs the day the penultimate egg in a clutch is laid. Males were captured and banded during the nestling period unless they were fortuitously captured earlier in the season. Each swallow was banded with a numbered U.S. Fish and Wildlife Service aluminum band and given a unique color mark by marking its tail, wings, forehead, throat, or breast feathers with a water-proof marking pen or acrylic paint.

Nest architecture.—Each year I began visiting nest boxes once a week during April to monitor nest building behavior. I began daily nest visits during the first week in May to monitor egg laying. The date of clutch initiation is reported as a Julian date (i.e. 1 January = 1). Once a clutch was completed I did not visit the nest again until I measured it during the second half of the 14-day incubation period. I waited until then to measure nests because males continue to add feathers to nests throughout most of the incubation period (Cohen 1985, pers. obs.). Using dial calipers, dividers, and a ruler, I measured to the nearest 1 mm the: (1) depth of nest material from top of nest to floor of box; (2) depth of nest material beneath nest cup; (3) depth of nest cup; (4) front-to-back diameter of top of nest cup (the front being the edge of cup parallel to side of nest box with the entrance hole); and (5) left-to-right diameter of top of nest cup.

Nest cup volume (V_c; mm³) was calculated as

$$V_c = ([4/3][\pi a^2 b]/2), \qquad (1)$$

where a is the largest radius (mm) of the top of the cup and b is cup depth (mm). This calculation assumed that the nest cup was one-half of an ellipsoid.

My nest-box trail contained boxes of two sizes: 25 had floors 10 cm × 14 cm and interior volumes of 1,736 cm³; 75 had floors 14 cm × 14 cm in area and interior volumes of 2,430 cm³. Hereafter, these boxes are classified as small and big, respectively. The distance from the floor to the ceiling of all boxes was 19.5 cm and the distance from the floor to the 4-cm-diameter entrance holes of all boxes was 12.4 cm. Total nest volume (V_n; cm³) was

$$V_n = LWD - V_c, \qquad (2)$$

where L, W, and D were length, width, and depth, respectively. The position of the nest-cup center was determined at each nest by comparing the location of the cup center with an imaginary grid of nine sectors (Fig. 1).

The feather content of each nest was scored on a scale of 0 to 4, with: (0) no feathers lining cup or woven into nest; (1) few scattered feathers that do not completely line cup; (2) a single layer of feathers lining cup; (3) two layers of feathers lining cup; and (4) more than two layers of feathers lining cup.

Eggs were numbered in sequence with indelible ink as they were laid. Egg length (l) and width (w) at the widest point of the egg were measured to the nearest 0.01 mm using a dial caliper. Egg volume (V_e; mm³) was calculated following Tatum (1975) as

$$\pi l w^2 / 6. \qquad (3)$$

The total egg volume (V_{et}) of an incubated clutch equaled the sum of the volumes of the eggs present during incubation. The cup index (C) estimated the degree of crowding of nest contents and was calcu-

lated as

$$C = V_e/V_c. \tag{4}$$

Reproductive performance.—To monitor reproductive performance I visited nests: (1) daily during egg laying to determine clutch size; (2) daily during the expected hatching period to determine the number of eggs that hatched; (3) when nestlings were 12 days old in order to band them; and (4) daily around the expected date of fledging to determine the number of nestlings that fledged.

Data analyses.—Data were analyzed using SAS (SAS Institute 1985). I tested for normality and homoscedasicity to determine the appropriate methods of analyses (Zar 1974). Most data sets were not normally distributed. I used the Wilcoxon two-sample test corrected for continuity to examine differences between means of populations. Some nest-architecture and reproductive-performance data were analyzed separately for each year because preliminary analyses showed among-year effects; only significant differences are reported. I performed multiple Wilcoxon two-sample tests corrected for continuity to detect yearly differences among measures of nest architecture and reproductive performance.

From 1988 to 1990, 28 females built two or more nests at the George Reserve. Of these, 9 females built 9 nests as subadults and later 10 nests as adult females (one subadult built two nests as an adult female). The remaining 18 females built 41 nests. Three adult females built three nests each. In order to avoid the confounding effects of statistical pseudoreplication (Hurlbert 1984), only the first nest built by each adult female at the George Reserve was used in statistical analyses. Successive nests built by females first as subadults and then as adult females in successive years were considered to be independent because no evidence of individual age-related patterns in nest construction was discovered.

RESULTS

Nests.—Tree Swallows took from one to three weeks to build their nests. At nests that I visited frequently enough during the nest-building period to determine the onset of nest building, there was no significant difference between subadult (14.80 ± SD of 6.01 days, $n = 25$) and adult females (12.43 ± 5.21 days, $n = 35$) in the number of days required to build nests (Wilcoxon $Z = 1.34$, $P > 0.10$). Females added nest material to boxes until approximately 30% of the nest box was filled (Table 1). Females added feathers to nests during the early stages of nest building and through egg laying (Cohen 1985). Males added few feathers during nest building and early egg laying, but enthusiastically added

TABLE 1. Female age, box size, and nest architecture (x̄ ± SD) in Tree Swallows using nest boxes. Wilcoxon two-sample tests corrected for continuity showed no significant differences between subadult and adult female nests in all measures of nest architecture except feather score (Wilcoxon $Z = 1.96$, $P = 0.051$). Wilcoxon two-sample tests corrected for continuity used to compare measures of nest architecture in big and small boxes (sizes given in text).

Nest architecture	Nests built by			Nest-box size		Wilcoxon Z
	Subadult females (n = 53)	Adult females (n = 72)	All nests (n = 125)	Big (n = 99)	Small (n = 27)	
Depth of nest material (mm)	40.47 ± 10.34	42.88 ± 9.15	41.86 ± 9.71	42.12 ± 9.05	40.85 ± 12.04	-0.18
Depth of nest cup (mm)	29.38 ± 9.21	31.00 ± 6.47	30.31 ± 7.76	30.36 ± 7.81	30.12 ± 7.72	-0.19
Depth of nest material beneath nest cup (mm)	11.09 ± 9.67	11.88 ± 8.34	11.54 ± 8.90	11.76 ± 8.88	10.73 ± 9.11	-0.72
Front-to-back diameter of top of nest cup (mm)	67.42 ± 8.92	67.46 ± 8.07	67.44 ± 8.41	67.90 ± 8.21	65.69 ± 9.07	-1.04
Left-to-right diameter of top of nest cup (mm)	68.85 ± 11.43	68.89 ± 8.98	68.76 ± 10.05	70.38 ± 9.61	62.58 ± 9.41	-3.56***
Nest-cup volume (mm³)	80.82 ± 37.95	84.88 ± 28.90	83.16 ± 32.96	86.88 ± 33.17	69.84 ± 28.99	-2.34*
Cup index	0.13 ± 0.10	0.13 ± 0.05	0.13 ± 0.05	0.12 ± 0.07	0.16 ± 0.09	2.13*
Total nest volume (cm³)	667.67 ± 197.10	706.13 ± 177.56	690.00 ± 186.20	727.94 ± 166.17	547.01 ± 191.15	-4.09***
Percentage of nest box filled with nest material	29.05 ± 7.91	30.34 ± 6.90	29.80 ± 7.34	29.96 ± 6.82	29.17 ± 9.16	-0.24
Feather score	2.96 ± 1.14	3.36 ± 0.90	3.19 ± 1.03	3.12 ± 1.05	3.44 ± 0.89	1.49

*, $P < 0.05$; ***, $P < 0.001$; other values not significant ($P > 0.05$).

many feathers throughout incubation and into the early stages of the nestling period (Sheppard 1977, Cohen 1985). Nest feather score was not significantly correlated with total nest volume ($r_s = -0.061$, $n = 124$, $P > 0.40$). Nest cups were usually completely formed and lined with a few feathers several days before the onset of egg laying.

Female age and nest architecture.—The nests of 53 subadult and 72 adult females were measured from 1988 to 1990. Although nests built by adult females were slightly larger than those of subadult females, there were no significant differences between female age-classes in nest size or volume (Table 1). Of the nine possible nest-cup positions, positions 2 and 5 were used the most often by both subadult and adult females (Fig. 1).

A greater proportion of nests built by adult females had two or more layers of feathers lining the cup (58/73 nests, 79%) than did nests built by subadult females (33/53 nests, 62%; $X^2 = 4.53$, $df = 1$, $P < 0.05$). Three nests (5.7%) built by subadult females had no feathers. In contrast, nests built by adult females always contained feathers.

Nest architecture and box size.—Big and small boxes were used with equal frequency by both subadult (big boxes had 42 nests, and small boxes had 13 nests) and adult females (big boxes had 60 nests, and small boxes had 14 nests; $X^2 = 0.42$, $df = 1$, $P > 0.50$).

Nest-box size affected nest architecture. Nests built in big boxes had significantly larger left-to-right cup diameters, cup volumes, and total nest volumes (Table 1). There was no difference between big and small boxes in the percentage of the nest-box volume filled with nest material (Table 1).

Nest-cup position was unaffected by box size, but nest cups were not randomly located inside of boxes ($X^2 = 3.73$, $df = 1$, $P > 0.05$). Nest cups were most often found in positions 2 and 5 (see Fig. 1) in both big (71/94 nests, 75.5%) and small (25/27 nests, 92.6%) boxes.

The relationship between box size and nest feathering was complex. Nests built by subadult females were equally well feathered in big (feather score, 2.85 ± 1.21, $n = 40$) and small (feather score, 3.31 ± 0.85, $n = 13$) boxes (Wilcoxon $Z = 1.11$, $P > 0.20$). Likewise, nests built by adult females were equally well feathered in big (feather score, 3.31 ± 0.90, $n = 59$) and small (feather score, 3.57 ± 0.94, $n = 14$) boxes

(Wilcoxon $Z = 1.31$, $P > 0.10$). Pooled together, the nests built by both subadult and adult females were equally well feathered in big (Wilcoxon $Z = -1.82$, $P > 0.05$) and small (Wilcoxon $Z = -1.10$, $P > 0.20$) boxes. Small boxes had a larger proportion of nests with two or more layers of feathers lining the cup (27/32 nests, 84%) than did big (69/99 nests, 70%; $X^2 = 8.76$, $df = 1$, $P < 0.005$) boxes.

Within-season variations in nest architecture.— The time of season when a nest was built influenced its architecture. For example, subadult females that constructed nests earlier in the season and began egg laying before the population median date of clutch initiation (Julian date = 138; 16 May) built nests that were of greater volume (before median date, 806.58 ± 197.07 cm³, $n = 13$; after median date, 621.37 ± 176.28 cm³, $n = 39$; Wilcoxon $Z = 2.49$, $P < 0.02$) and had more material beneath the nest cup floor (before median date, 17.85 ± 14.04 mm, $n = 13$; after median date, 8.90 ± 6.62 mm, $n = 40$; Wilcoxon $Z = 2.08$, $P < 0.04$).

In contrast, there was little within-season variation in the nest architecture of nests built by adult females. Adult females that began egg laying before the population median date of clutch initiation built nest cups of greater volume (before median date, 90.21 ± 26.92 cm³, $n = 44$; after median date, 76.51 ± 30.38 cm³, $n = 28$; Wilcoxon $Z = -2.45$, $P < 0.02$). This difference was not due to larger adult female clutch sizes earlier in the season because there was no significant difference between adult female clutch sizes laid either before (5.62 ± 1.05, $n = 45$) or after (5.55 ± 0.78, $n = 29$) the median date of clutch initiation (Wilcoxon $Z = -1.03$, $P > 0.30$). Contrary to prediction, there was no correlation between nest feather score and the date of clutch initiation at nests built by either subadult ($r_s = -0.025$, $n = 53$, $P > 0.80$) or adult females ($r_s = 0.22$, $n = 72$, $P > 0.05$).

Nest architecture and reproductive success.—Reproductive performance in Tree Swallows is influenced by a breeding female's age (DeSteven 1978, 1980, Stutchbury and Robertson 1988, this study) and time in the season when she begins egg laying (Stutchbury and Robertson 1988, this study). On average, subadults began clutches later (Julian date 143.55 ± 9.65) than did adult females (Julian date 137.43 ± 5.32; Wilcoxon $Z = 4.29$, $P < 0.0001$). At the George Reserve, reproductive performance was also associated with nest architecture.

At nests built early in the season by subadult females, the front-to-back diameter of the top of the nest cup was positively correlated with clutch size ($r_s = 0.65$, $n = 13$, $P < 0.02$). Later in the season, the nest volume of nests built by subadult females was positively correlated with the number of eggs that hatched ($r_s = 0.35$, $n = 32$, $P < 0.05$). Likewise, the greater the percentage of the nest box filled with material, the more eggs hatched ($r_s = 0.50$, $n = 32$, $P < 0.005$) and the larger the proportion of eggs hatched ($r_s = 0.37$, $n = 38$, $P < 0.03$). The depth of material beneath the nest-cup floor was also positively correlated with the number ($r_s = 0.44$, $n = 32$, $P < 0.05$) and proportion of eggs ($r_s = 0.34$, $n = 39$, $P < 0.05$) that hatched. However, feather score was not correlated with the production of nestlings ($P > 0.10$) or fledglings ($P > 0.80$).

There were no significant correlations between nest architecture and reproductive performance at nests where adult females began to lay eggs before the median date of clutch initiation. However, nest architecture was correlated with the reproductive performance of adult females later in the season; cup volume was positively correlated with the number of fledglings produced ($r_s = 0.53$, $n = 18$, $P < 0.03$) and the proportion of hatchlings that fledged at each nest ($r_s = 0.56$, $n = 19$, $P < 0.02$). However, the more crowded the cup (as indicated by the cup index) the fewer young that fledged ($r_s = -0.54$, $n = 18$, $P < 0.03$) and the smaller the proportion of the hatchlings that fledged ($r_s = -0.62$, $n = 18$, $P < 0.007$).

Correlations between nest architecture and reproductive performance varied within the breeding season each year; in 1990 at subadult females' nests and in 1989 and 1990 at adult females' nests. When subadult females began egg laying after the median date of clutch initiation in 1990, the depth of nest material beneath the nest-cup floor was positively correlated with brood size at hatching ($r_s = 0.66$, $n = 12$, $P < 0.02$) and the proportion of the clutch that hatched at each nest ($r_s = 0.71$, $n = 12$, $P < 0.01$). Likewise, the percentage of the box filled by the nest was positively correlated with the brood size at hatching ($r_s = 0.69$, $n = 12$, $P < 0.02$) and the proportion of the clutch that hatched at each nest ($r_s = 0.74$, $n = 12$, $P < 0.006$). However, the depth of nest material beneath the nest-cup floor was negatively correlated with brood size at fledging ($r_s = -0.77$,

$n = 11$, $P < 0.001$) and the proportion of hatchlings that fledged ($r_s = -0.85$, $n = 11$, $P < 0.001$). The proportion of the box filled with nest material was negatively correlated with the proportion of hatchlings that fledged ($r_s = -0.65$, $n = 11$, $P < 0.04$).

There were no significant correlations between nest architecture and reproductive performance at nests where adult females began egg laying before the median date of clutch initiation in 1989. However, at nests where adult females began egg laying after the median date of clutch initiation, the depth of the nest material below the cup was negatively correlated with the proportion of eggs that hatched ($r_s = -0.81$, $n = 8$, $P < 0.05$), but nest crowding (as measured by cup index) was positively correlated with the proportion of eggs that hatched ($r_s = 0.82$, $n = 6$, $P < 0.05$). At nests where adult females began egg laying before the median date of clutch initiation in 1990, birds that filled more of the nest box with material produced more fledglings ($r_s = 0.68$, $n = 9$, $P < 0.05$). However, brood size at hatching was negatively correlated with the depth of nest material ($r_s = -0.61$, $n = 15$, $P < 0.05$), the nest volume ($r_s = -0.63$, $n = 15$, $P < 0.05$), and the percentage of the box filled with material ($r_s = -0.72$, $n = 15$, $P < 0.005$). In addition, cup index was negatively correlated with the proportion of hatchlings that fledged ($r_s = -0.59$, $n = 12$, $P < 0.05$).

DISCUSSION

General nest architecture.—The nests of Tree Swallows in southeastern Michigan were composed of a mat of dry grasses about 40 mm deep (Table 1) with a nest cup lined with feathers. The material in these nests was about 10 mm deeper than in the deepest nests built by swallows near Lake Oneida, New York (Sheppard 1977). Although nest linings are usually thicker in cold climates (Collias and Collias 1984), during the period when most nests were built (i.e. before the population median date of clutch initiation in each area) the average mean daily temperature was greater ($Z = 3.72$, $P < 0.001$) in Michigan ($12.9 \pm 1.6°C$, NOAA 1988, 1989, 1990) than in New York ($10.1 \pm 2.9°C$, Sheppard 1977:fig. 13). It is possible that birds may adjust the insulative qualities of their nests by constructing either tightly or loosely woven nests in response to air temperatures during the nest-building period. Unfortunately, neither Shep-

pard (1977) nor I estimated whether nests were either tightly or loosely woven, making it impossible to test this hypothesis.

Nest cups located in the center of the box are surrounded by nest material on all sides and should be better insulated than nest cups that are located against a nest box wall. Nest cups located in the center of the nest box are easily reached by parents feeding nestlings, but also by predators such as racoons that typically reach into the box and pull out its contents. Therefore, there are both advantages and disadvantages to building nests with cups located in the center of the box. Nest cups located in the middle of the back wall may not be as well insulated but are slightly more difficult for predators to reach. Neither Sheppard (1977:table 17) nor I found nests with nest cups directly below the nest-box hole, the position most easily reached by a nest predator.

The depth of nest material used by cavity-nesting birds may reflect a trade-off between the thermal benefits of a thick nest and disadvantage of placing the nest contents within the easy reach of nest predators. Interestingly, House Wrens (Troglodytes aedon) that build nests in boxes typically fill the box up to the bottom edge of the hole with material (Kennedy and White 1992), potentially placing the nest contents within the easy reach of nest predators.

Female age and nest architecture.—I found few differences in architecture between the nests built by subadult and adult female Tree Swallows. There were no significant differences between subadult and adult female nests in the physical dimensions of the mat of dry grasses or in the time it took to build the nest, but nests built by subadults were slightly smaller and took slightly longer to build than those built by adult females. No statistical patterns in nest dimensions were noted in nests of individuals that built multiple nests during the course of the study. These results suggest that experience has less influence on nest-building behavior in Tree Swallows than in weavers (Ploceidae; Collias and Collias 1964, 1984) or Zebra Finches (Taeniopygia guttata; Sargent 1965). However, more subadult ($n = 4$) than adult females ($n = 1$) built rudimentary nests and laid eggs on the wooden floor of the nest box, suggesting that some subadults may be inferior nest builders. Alternatively, subadult female Tree Swallows may build rudimentary nests because they begin nest building later in the season than adult

females and, therefore, may rush nest building in order to begin egg laying before late June when the window of opportunity for successful reproduction closes (unpubl. data).

The nests of Tree Swallows typically contain feathers lining the cup and accumulated throughout the nest material. I did not count feathers in nests. Sheppard (1977) found that most nests had from 25 to 50 feathers (range 0 to 150). These feathers probably provide a thermal benefit. Winkler (1993) found that nestlings in well-feathered nests had faster growth rates than nestlings in nests where he experimentally removed feathers. Neither Winkler (1993) nor I found a significant correlation between nest feather score and the number or proportion of hatchlings and fledglings produced.

Nest feathers may serve as a barrier between the nestlings and nest ectoparasites. Cohen (1988) argued that nest feathers were an anti-ectoparasite adaptation in Tree Swallows because the energy expended competing for nest feathers outweighed their thermal benefits in the nest. Winkler (1993) also showed that nest feathers also may provide a benefit against nest ectoparasites. I did not compare feather scores with nest ectoparasite loads. However, Capreol (1983 *in* Rogers et al. 1991) found no correlation between nest feather number and *Protocalliphora sialia* (Diptera: Calliphoridae) parasite loads in the nests of Tree Swallows. Møller (1987) found no association between the number of feathers lining Barn Swallow nests and the number of haematophagous mites found in the nest.

The nests built by subadult and adult females differed most in the amount of feathers found lining the nest cup (Table 1). Because competition for nest feathers is intense in Tree Swallows (Gibbs 1981, Cohen 1985, 1988) and fights over feather ownership are common (Winkler 1993, pers. obs.), the amount of feathers found in nests may reflect the competitive abilities of the nest owners (Sheppard 1977, Gibbs 1981). However, there were no significant correlations between nest feather score and nest-owner size, except at the nests built by subadult females; subadult female wing length was negatively correlated with nest feather score (unpubl. data). The biological significance of this relationship is not clear.

Most feathers that males collect are obtained by retrieving feathers that are floating in the air. Males typically do not retrieve feathers from

the ground, especially if the vegetation is deep (Cohen 1985, pers. obs.). Fights over feathers are often long aerial battles in which feather owners and their pursuers fly very fast and change direction rapidly and often. These observations suggest that flying skill is an important component of feather-gathering ability in male Tree Swallows. Interestingly, there were no correlations between any measure of male size and nest feather score (unpubl. data), suggesting that male size, within normal variation, provided neither an advantage nor disadvantage in competing for feathers. However, the differences in nest feathering at nests built by subadult and adult females suggest that males mated to subadults are inferior to males mated to adult females in feather competition. Male Tree Swallows cannot be aged by plumage characters, but based on yearly migratory-return patterns (i.e. yearlings return to breeding areas later in the season than do older Tree Swallows; Cohen 1978), it is likely that subadult females are mated to younger males than are adult females. Males mated to subadult females are the same size as males mated to adult females (unpubl. data), suggesting that skill gained through experience is an important component in male feather gathering ability.

Nest-box size.—Nest-box size affected nest architecture. Nests in big boxes contained more nest material than those built in small boxes (Table 1), but Tree Swallows filled approximately 30% of the available cavity space, regardless of box size (Table 1). There are behavioral and energetic consequences of this behavior: big boxes would have required more effort to fill than small boxes. However, this increased effort did not affect reproductive performance. There were no statistically significant differences in reproductive performance between swallows nesting in big or small boxes. Cohen (1977) also found no effect on Tree Swallow reproductive performance in the Colorado Rocky Mountains. There were no associations between nest-box size and reproductive performance that could not also be explained by female age and within-season variation in reproductive performance. In contrast, many studies of other species of hole-nesting birds have found a positive correlation between clutch size and the area of the nest-box floor (e.g. Karlsson and Nilsson 1977, van Balen 1984, Gustafsson and Nilsson 1985, Slagsvold 1987; but see Alatalo et al. 1988). Robertson and Rendell (1990)

found that Ontario Tree Swallows in nest boxes laid larger clutches than did those using natural cavities. They argued that this was because floor area was smaller in natural cavities. In their study, the floor area of nest boxes was twice as large as the mean floor area of natural cavities. In mine, big floors were 40% larger than the small floors and may not have differed enough to influence female swallows to adjust their clutch sizes. Additionally, nest-box-trail operators usually clean out old nesting material from boxes before each season. In contrast, natural cavities accumulate nest material each year, thus shrinking the available space, which could have a negative influence on clutch size. The best way to test these hypotheses is with an experiment that controls for differences in parental quality.

Nest architecture and reproductive performance.—Reproductive performance was associated with variations in nest architecture. Early in the season, the front-to-back diameter of the top of the nest cups built by subadult females was positively correlated with clutch size, suggesting that subadult females that laid larger clutches modified their nests to accommodate more eggs. Later in the season, several aspects of the architecture of nests built by subadult females were significantly correlated with various measures of reproductive performance. In general, larger nests produced more nestlings, suggesting that the amount of nest material collected may have positively affected the ability of subadult females to hatch their eggs. Interestingly, nest feather score was not correlated with the production of either hatchlings or fledglings despite the insulative quality of feathers.

Nest architecture was not correlated with adult female reproductive performance early in the season. This result is surprising because nest insulation should influence reproductive performance early in the season when average ambient temperatures during incubation are lower and there is greater daily variation in ambient temperatures. The contents of poorly insulated nests cool quickly at low ambient temperatures, forcing incubating birds to expend more energy and time reheating eggs when they return to nests; they then are left with less time between bouts of incubation for foraging (White and Kinney 1974). However, endothermic nestlings risk hyperthermia when crowded into a well-insulated nest late in the season when average

ambient temperatures are higher (Mertens 1977b). The cup index was negatively correlated with both brood size at fledging and the proportion of hatchlings that fledged late in the season, suggesting that hyperthermia due to overcrowding of nestlings was a factor affecting the reproductive performance of adult females late in the season.

Little of the yearly within-season variation in nest architecture was significantly correlated with reproductive performance except in 1990. Subadult females that built larger nests (as indicated by depth on nest material beneath the cup and percentage of the box filled with material) produced more hatchlings per nest than did those with smaller nests. However, larger nests were a disadvantage in terms of producing fledglings later in 1990 because the depth of nest material beneath the nest-cup floor and the percent of box filled with nest material were both negatively correlated with brood size at fledging and the proportion of young that fledged. Hyperthermia correlated with the insulative quality of larger nests may have affected the reproductive performance of late-breeding subadult females. Subadult females are more likely to begin clutches after the population median date of clutch initiation (Stutchbury and Robertson 1988, this study).

Within-season variations in nest architecture were associated with variations in the reproductive performance of adult females in 1989 and 1990. Late in the season in 1989, the nests of adult females with more material beneath the nest cup hatched a significantly smaller proportion of eggs, whereas those with crowded nest cups hatched a significantly larger proportion of eggs. Neither the depth of nest material below the cup nor nest cup crowding were significantly correlated with fledging success. However, early in the season in 1990, larger nests (as indicated by the percentage of the nest box filled with material) appeared to be advantageous because they produced more fledglings than smaller nests. However, larger nests were disadvantageous later in the season because they produced fewer hatchlings and, consequently, fewer fledglings than smaller nests. The negative correlation between the cup index and the proportion of hatchlings that fledged indicates that hyperthermia induced by the crowding of nestlings may have affected the reproductive performance of late-breeding adult females (e.g. Møller 1987). My results suggest that experi-

ments involving manipulation of nest insulation, clutch size during incubation, and brood size during the nestling period could reveal interesting information about incubation and nestling energetics in Tree Swallows.

LITERATURE CITED

ALATALO, R. V., A. CARLSON, AND A. LUNDBERG. 1988. Nest cavity size and clutch size of Pied Flycatchers *Ficedula hypoleuca* breeding in natural tree holes. Ornis Scand. 19:317–319.

BROWN, C. R., AND M. B. BROWN. 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). Ecology 67:1206–1218.

BURTT, E. H., JR., W. CHOW, AND G. A. BABBITT. 1991. Occurrence and demography of mites of Tree Swallow, House Wren, and Eastern Bluebird nests. Pages 104–122 in Bird-parasite interactions: Ecology, evolution, and behaviour (J. E. Loye and M. Zuk, Eds.). Oxford Univ. Press, New York.

CALDER, W. A. 1971. Temperature relationships and the nesting of the Calliope Hummingbird. Condor 73:314–321.

CALDER, W. A. 1973. An estimate of the heat balance of a nesting hummingbird in a chilling climate. Comp. Biochem. Physiol. 46A:291–300.

CAPREOL, M. 1983. The adaptive significance of the feather lining in the Tree Swallow (*Tachycineta bicolor*) nest and its effect on reproductive success. B.S. thesis, Queen's Univ., Kingston, Ontario.

CLARK, L. 1991. The nest protection hypothesis: The adaptive use of plant secondary compounds in European Starlings. Pages 205–221 in Bird-parasite interactions: Ecology, evolution, and behaviour (J. E. Loye and M. Zuk, Eds.), Oxford Univ. Press, New York.

COHEN, R. R. 1977. On the breeding ecology of the Tree Swallow, *Iridoprocne bicolor*, in the Colorado Rocky Mountains. J. Colo.-Wyo. Acad. Sci. 9:47.

COHEN, R. R. 1978. Behavioral adaptations for cavity-nesting in the Tree Swallow (*Iridoprocne bicolor*). J. Colo.-Wyo. Acad. Sci. 10:50.

COHEN, R. R. 1985. Capturing breeding male Tree Swallows with feathers. N. Am. Bird Bander 10: 18–21.

COHEN, R. R. 1988. Is feather-gathering by nesting swallows mainly an anti-ectoparasite tactic? J. Colo.-Wyo. Acad. Sci. 20:9.

COLLIAS, E. C., AND N. E. COLLIAS. 1964. The development of nest-building behavior in a weaverbird. Auk 81:42–52.

COLLIAS, N. E., AND E. C. COLLIAS. 1984. Nest building and bird behavior. Princeton Univ. Press, Princeton, New Jersey.

DeSTEVEN, D. 1978. The influence of age on the breeding biology of the Tree Swallow, *Iridoprocne bicolor*. Ibis 120:516–523.

DeSTEVEN, D. 1980. Clutch size, breeding success, and parental survival in the Tree Swallow. Evolution 34:278–291.

DILGER, W. C. 1962. The behavior of lovebirds. Sci. Am. 206(1):88–99.

DWIGHT, D., JR. 1900. The sequence of plumages and molts of passerine birds of New York. Ann. N.Y. Acad. Sci. 13:73–360.

GIBBS, H. L. 1981. An experimental analysis of social behavior in breeding Tree Swallows (*Iridoprocne bicolor*). M.S. thesis, Univ. Michigan, Ann Arbor, Michigan.

GUSTAFSSON, L., AND S. G. NILSSON. 1985. Clutch size and breeding success of Pied and Collared flycatchers *Ficedula* spp. in nest-boxes of different sizes. Ibis 127:380–385.

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187–211.

HUSSELL, D. J. T. 1983. Age and plumage color in female Tree Swallows. J. Field Ornithol. 54:312–318.

KARLSSON, J., AND S. G. NILSSON. 1977. The influence of nest-box area on clutch size in some hole-nesting passerines. Ibis 119:207–211.

KENNEDY, E. D., AND D. W. WHITE. 1992. Nest building in House Wrens. J. Field Ornithol. 63:35–42.

KUERZI, R. G. 1941. Life history studies of the Tree Swallow. Proc. Linn. Soc. N.Y. 52-53:1–52.

MASON, E. A. 1944. Parasitism by *Protocalliphora* and management of cavity-nesting birds. J. Wildl. Manage 8:232–247.

MERTENS, J. A. L. 1977a. Thermal conditions for successful breeding in Great Tits (*Parus major* L.). II. Thermal properties of nests and nest boxes and their implications for the range of temperature tolerance of Great Tit broods. Oecologia (Berl.) 28:31–56.

MERTENS, J. A. L. 1977b. Thermal conditions for successful breeding in Great Tits (*Parus major* L.). Oecologia (Berl.) 28:1–29.

MØLLER, A. P. 1982. Clutch size in relation to nest size in the Swallow *Hirundo rustica*. Ibis 124:339–343.

MØLLER, A. P. 1984. On the use of feathers in birds' nests: Predictions and tests. Ornis Scand. 15:38–42.

MØLLER, A. P. 1987. Nest lining in relation to the nesting cycle in the Swallow *Hirundo rustica*. Ornis Scand. 18:148–149.

MOSS, W. W., AND J. H. CAMIN. 1970. Nest parasitism, productivity, and clutch size in Purple Martins. Science 168:1000–1003.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA). 1988. Climatological data, Michigan, vol. 103, no. 5. National Climatic Data Center, Asheville, North Carolina.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA). 1989. Climatological data, Michigan, vol. 104, no. 5. National Climatic Data Center, Asheville, North Carolina.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA). 1990. Climatological data, Michigan, vol. 105, no. 5. National Climatic Data Center, Asheville, North Carolina.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. Ornis Scand. 15:167–175.

O'CONNOR, R. J. 1978. Nest box insulation and the timing of laying in Wytham Woods population of Great Tits *Parus major*. Ibis 120:534–537.

RENDELL, W. B., AND R. J. ROBERTSON. 1989. Nest-site characteristics, reproductive success, and cavity availability for Tree Swallows breeding in natural cavities. Condor 91:875–885.

ROBERTSON, R. J., AND 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.

ROGERS, C. A., R. J. ROBERTSON, AND B. J. STUTCHBURY. 1991. Patterns and effects of parasitism by *Protocalliphora siala* on Tree Swallow nestlings. Pages 123–139 *in* Bird-parasite interactions: Ecology, evolution, and behaviour (J. E. Loye and M. Zuk, Eds.). Oxford Univ. Press, New York.

SARGENT, T. D. 1965. The role of experience in the nest building of the Zebra Finch. Auk 82:48–61.

SAS INSTITUTE. 1985. SAS user's guide: Statistics, version 5 ed. SAS Institute, Inc., Cary, North Carolina.

SHEPPARD, C. D. 1977. Breeding in the Tree Swallow, *Iridoprocne bicolor*, and its implications for the evolution of coloniality. Ph.D. dissertation, Cornell Univ., Ithaca, New York.

SKOWRON, C., AND M. KERN. 1980. The insulation in nests of selected North American songbirds. Auk 97:816–824.

SLAGSVOLD, T. 1987. Nest site preference and clutch size in the Pied Flycatcher *Ficedula hypoleuca*. Ornis Scand. 18:189–197.

STUTCHBURY, B. J., AND R. J. ROBERTSON. 1988. With-

in-season and age-related patterns of reproductive performance in female Tree Swallows (*Tachycineta bicolor*). Can. J. Zool. 66:827–834.

TATUM, J. B. 1975. Egg volume. Auk 92:576–580.

VAN BALEN, J. H. 1984. The relationship between nest-box size, occupation and breeding parameters of the Great Tit *Parus major* and other hole-nesting species. Ardea 72:163–175.

WAINWRIGHT, S. A., W. D. BRIGGS, J. D. CORREY, AND J. M. GOSLINE. 1976. Mechanical design in organisms. J. Wiley, New York.

WALSBERG, G. E., AND J. R. KING. 1978. The energetic consequences of incubation for two passerine species. Auk 95:644–655.

WHITE, F. N., AND J. L. KINNEY. 1974. Avian incubation. Science 186:107–115.

WINKLER, D. W. 1993. Use and importance of feathers as nest lining in Tree Swallows (*Tachycineta bicolor*). Auk 110:29–36.

ZAR, J. H. 1974. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey.