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EFFECT OF FEATHERS AS NEST INSULATION ON INCUBATION BEHAVIOR AND REPRODUCTIVE PERFORMANCE OF TREE SWALLOWS (*TACHYCINETA BICOLOR*)

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ABSTRACT.—Many species of birds line their nests with feathers, presumably because of the insulative qualities of feathers and because feathers may act as a barrier between nest parasites and nestlings. In 1993, we experimentally examined the role of feathers as nest insulation on the incubation behavior, nestling growth, and reproductive performance of Tree Swallows (*Tachycineta bicolor*) nesting in boxes in western Michigan. There were no significant differences between the incubation rhythms of females with experimental nests (i.e. no feathers) and females with control nests (i.e. with feathers). Nestlings that were reared in control nests had significantly longer right tarsi and right wing chords; their masses were significantly greater than nestlings reared in experimental nests. In addition, nested analyses of variance indicated that both female age class (i.e. second year, after second year, or after hatching year) and the brood within which a nestling was reared had significant effects on nestling growth until nestling day 12. Whether an individual nestling was infected with ectoparasites was independent of whether it was reared in an experimental or control nest. Nest insulation affected reproductive performance: females with experimental nests had significantly longer incubation periods and produced significantly fewer fledglings than did females with control nests. These results suggest that nest insulation may be an important factor influencing incubation behavior, nestling growth, and reproductive performance of Tree Swallows in western Michigan. *Received 21 November 1994, accepted 21 June 1995.*

NESTS ARE an important component of parental effort in birds. Nests provide safety from predators, and a container and microenvironment for incubating parents, developing eggs, and nestlings (Collias and Collias 1984). Nest building is influenced by "instinct" and learning: the nests of experienced birds often are superior to those built by novices (Collias and Collias 1984). Determining the consequences of individual differences in nest architecture on reproductive performance are important to a complete understanding of the factors affecting the evolution of parental effort in birds.

Tree Swallows (*Tachycineta bicolor*) 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 many of the feathers that line the cup (Sheppard 1977, Cohen 1985). The nests of second-year females are less well feathered than nests built by after-second-year females (Lombardo 1994). Differences in nest feathering may influence the age-related differences in reproductive performance that have been observed in Tree Swallows (DeSteven 1978, 1980, Stutchbury and Robertson 1988) because of the effects of feathers on the thermoenergetics of incubation, brooding, and nestling growth.

Winkler (1993) experimentally examined the effect of feathers as nest insulation on reproductive performance in Tree Swallows nesting in boxes near Ithaca, New York, and found that feathers as nest lining had no effect on fledging success, but nestlings reared in control nests (i.e. with feathers) were larger on the twelfth nestling day, fledged earlier, and had fewer ectoparasites than those reared in experimental nests (i.e. without feathers). He did not examine whether there were female age-related differences in reproductive performance that were influenced by feathers as nest insulation. Lombardo (1994) did a correlational study of nest architecture, female age, and reproductive performance of Tree Swallows nesting in southeastern Michigan and found no relationship between the amount of nest feathering and the number or proportion of hatchlings and fledglings produced. However, well-insulated nests were advantageous early in the season when ambient temperatures were low and eggs and nestlings needed to be kept warm, but disadvantageous late in the season when ambient

temperatures were higher and nestlings in well-insulated nests overheated (Lombardo 1994). Neither Winkler (1993) nor Lombardo (1994) examined the influence of feathers as nest insulation on incubation behavior.

The main purpose of our study was to examine experimentally the effect of feathers as nest insulation on incubation rhythms in Tree Swallows nesting in boxes in western Michigan. Despite being a well-known species in many respects, relatively little is known about the incubation behavior of Tree Swallows (Robertson et al. 1992). Therefore, one of our goals was to study the incubation behavior of this species. In order to compare the results of our study with those of Winkler (1993) and Lombardo (1994), we also examined the influence of feathers as nest lining on reproductive performance and ectoparasite loads on nestlings.

METHODS

In 1993, we studied Tree Swallows nesting in some of the 100 wooden nest boxes mounted on metal poles erected in grids in old fields on the campus of Grand Valley State University in Ottawa County, western Michigan (42°57′N, 85°53′W). Each nest box is at least 30 m from its nearest neighbor, spacing similar to that found in a Canadian population of Tree Swallows nesting in natural cavities (Robertson and Rendell 1990). All nest-box entrance holes faced south. We deterred nest predators (e.g. raccoons, *Procyon lotor*) from destroying nests by applying axle grease to nest poles before the start of the breeding season.

Based on plumage characteristics breeding female Tree Swallows were categorized as second year (SY, mostly brown dorsal plumage), after second year (ASY, mostly iridescent blue-green dorsal plumage), or after hatching year (AHY, intermediate plumage; Hussell 1983). Males develop the full adult breeding plumage before their first winter (Dwight 1900).

Breeding females and males were captured at their nests during egg laying. 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 manipulations.—We monitored the breeding activity of the Tree Swallows by checking nest boxes once daily late in the morning during egg laying. Tree Swallows typically lay eggs early in the morning (Robertson et al. 1992). Eggs were numbered with indelible ink as laid. When egg laying was completed at each nest, it was assigned to either the experimental or control group. Nests alternately were assigned to the two groups to avoid any seasonal bias in the results. Following Winkler (1993), we removed feathers daily from each experimental nest from the day of clutch completion until its nestlings were 12 days old. To ensure that all control nests had a similar level of insulation, we manipulated the number of feathers in control nests, so that at least three layers of feathers lined the cup. Removing feathers from experimental nests disturbed them. To control for this disturbance, we also visited control nests daily until nestlings were 12 days old. At each visit we manipulated nest material, eggs, and nestlings to simulate the disturbance at experimental nests.

To avoid the confounding effects that clutch size might have on incubation rhythm (Biebach 1984), we standardized clutch sizes in both experimental and control nests to five eggs by either adding or removing eggs. Eggs added to nests were obtained from nearby nests and were matched in age by their laying dates with the eggs in the recipient nests. Burtt (1977) showed by experiment that neither egg manipulations nor the presence of foreign conspecific eggs affected the duration of incubation in Tree Swallows.

Incubation rhythm.—We observed the incubation behavior of females on the fifth, seventh, ninth, eleventh, and thirteenth day of incubation at each nest; incubation typically lasts 14 days (Robertson et al. 1992). During each 60-min observation period, we used binoculars to observe behavior from seats in the open about 30 m away from focal nests. Complete incubation bouts were recorded when we observed a female enter a nest box at the start of the bout and exit at its completion. Incomplete bouts were recorded when either we began an observation period and subsequently observed a female exit terminating a bout, or when we ended an observation period while an incubating female was still in the box. We determined time budgets of incubating females by recording to the nearest 30 s the amount of time females spent: (1) inside boxes out of our view, presumably incubating eggs; (2) perched; and (3) flying. When birds were out of sight, we assumed that they were flying. When flying, Tree Swallows are usually foraging for insects. Time budgets in Tree Swallows accurately reflect energy expenditures (Williams 1988).

Environmental conditions.—We determined air temperatures inside and outside of nest boxes during observation periods because ambient temperatures may influence incubation rhythm. At the beginning of and immediately after each observation period, we determined the ambient air temperature outside of the nest box and the air temperature inside the box just above the cup of the nest. We averaged the inside and outside temperatures recorded during each observation period to use in analyses. We determined temperatures using either mercury thermometers read to the nearest 1°C or electronic Rotemp digital TM 99A thermometers read to the nearest 0.1°C.

At the start of each observation period, we scored weather conditions on a subjective scale. Cloud cover was categorized and scored as: (1) none, (2) partly

TABLE 1. Mean incubation bout length (min) at experimental (i.e. without feathers) and control (i.e. with feathers) nests of SY and ASY female Tree Swallows. Student's t-tests used to compare means of mean incubation bout lengths per nest between experimental and control nests (rows) and between SY and ASY females (columns).

Female age	Nests without feathers (no. females; bouts)	Nests with feathers (no. females; bouts)	Student's t
SY	14.06 ± 4.66 (5; 48)	14.14 ± 2.37 (7; 65)	0.06^{ns}
ASY	14.22 ± 3.51 (7; 70)	10.67 ± 5.72 (5; 41)	1.34^{ns}
Student's t	0.09^{ns}	1.46^{ns}	

^{ns}, $P > 0.05$.

cloudy, (3) mostly cloudy, or (4) overcast. Precipitation was categorized and scored as: (1) none, (2) light rain, or (3) steady rain. Wind conditions were categorized and scored as: (1) none, (2) light when leaves in trees fluttered, (3) medium when branches in trees swayed, or (4) heavy when trees swayed in the wind. We observed incubating birds under all weather conditions.

Reproductive performance.—We monitored reproductive performance at each nest by recording the length of the incubation period (measured as number of days from day eggs were first warm to our touch until day first egg in a clutch hatched), number of eggs hatched, length of the nestling period (measured as number of days from when first egg in clutch hatched until last nestling in brood fledged), and the number of fledglings produced.

Nestling growth and ectoparasite loads.—Following Winkler (1993), we measured nestlings when they were banded at 12 days of age. Nestlings were individually weighed to the nearest 0.5 g using a Avinet spring scale. The right tarsus of each nestling was measured to the nearest 0.01 mm with a Mitutoyo Digimatic electronic caliper. The flattened right wing-chord length of each nestling was measured to the nearest 1.0 mm with a ruler. Each nestling was searched for lice, mites, and the larvae of parasitic flies (e.g. *Protocalliphora* spp.).

Statistical analyses.—Data were analyzed using SAS (SAS Institute 1985). To avoid statistical pseudoreplication in examining the effects of the removal of nest feathers on incubation behavior, we used mean incubation bout length at each nest in our analyses. We tested all data sets for normality and homoscedasticity to determine the appropriate methods of analyses (Zar 1974). Most data sets were not normally distributed, so we used nonparametric tests to detect differences between the means of data sets. A Student's t-test was used to detect differences between the means of normally distributed data sets. Spearman's rank correlation coefficients (r_s) were used to examine correlations between incubation behavior and ambient air temperatures, nest-box air temperatures, and weather conditions. To determine whether female age class and the brood within which a nestling was reared affected its growth until nestling day 12, we used nested analyses of variance on the ranks of nestling tarsus length, wing-chord length, and mass (Zar 1974). Data are reported as $\bar{x} \pm 1$ SD.

RESULTS

Incubation behavior.—Incubation began the day penultimate eggs were laid at 7 nests, the day the last egg of the clutch was laid at 17 nests, the day after the last egg was laid at 2 nests, and 2 days after the last egg was laid at 1 nest. Data on incubation behavior from all females were pooled because: (1) we observed no significant differences in incubation rhythm between females at experimental or control nests, or between SY and ASY females (Table 1); (2) there were no differences among SY, ASY (Table 1), or AHY (n = 2 experimental nests, n = 1 control nest) females during 137 h of observations at 14 experimental (75 h) and 13 control (62 h) nests; and (3) there was no significant difference in mean date of clutch initiation between SY (Julian date, 138.5 ± 14.2) and ASY (129.8 ± 2.3) females (Mann-Whitney U = 47, P = 0.16). Females spent on average 42.99 ± 9.51 min/h incubating eggs. Of the 16.93 ± 9.42 min/h spent off the eggs, females spent 1.95 ± 4.17 min perching and 14.92 ± 9.32 min flying. The day in the incubation period had no effect on the amount of time females spent outside of boxes during observation periods (r_s = 0.005, n = 137, P = 0.95), or the time they spent perching (r_s = −0.062, n = 137, P = 0.47), or flying (r_s = 0.023, n = 137, P = 0.79).

Environmental factors and incubation behavior.—Cloud cover, precipitation, and wind had no significant effect on female time in box, time out of box, flying, or perching (all $P > 0.05$) during each observation period. On average, air temperatures inside of boxes were significantly warmer than ambient air temperatures; the mean difference was 0.90 ± 1.23°C warmer inside box-

TABLE 2. Reproductive performance at experimental (i.e. no feathers; $n = 12$) and control (i.e. with feathers; $n = 12$) SY and ASY female nests. All nests given clutch size of five eggs at start of incubation. Measures of reproductive performance represented as $\bar{x} \pm$ SD. Wilcoxon two-sample test corrected for continuity used to compare means.

Measure of reproductive performance	Nests without feathers	Nests with feathers	Wilcoxon Z
Incubation length (days)	13.21 ± 0.70	12.40 ± 0.84	−2.27*
Number of eggs hatched	3.57 ± 1.16	4.20 ± 0.79	1.31^{ns}
Brood size on nestling day 12	2.15 ± 1.91	3.70 ± 1.64	1.82^{ns}
Length of nestling period (days)	22.33 ± 2.00	20.78 ± 0.83	1.75^{ns}
Number of fledglings	2.08 ± 1.56	3.60 ± 1.58	2.16*

*, $P < 0.05$; ^{ns}, $P > 0.05$.

es (paired t-test, $t = -8.52$, $n = 137$, $P < 0.001$). However, these differences between inside and outside air temperatures were not significantly different at experimental and control nests (Wilcoxon $Z = 0.41$, $n = 137$, $P > 0.6$). The amount of time females spent inside boxes incubating eggs was negatively correlated with mean ambient air temperatures outside of boxes during observation periods ($r_s = -0.22$, $n = 136$, $P = 0.009$). When outside, the amount of time females spent flying was positively correlated with air temperature during observation periods ($r_s = 0.28$, $n = 136$, $P < 0.001$). The amount of time females spent inside the nest box was negatively correlated with the air temperature inside of the nest box during observation periods ($r_s = -0.25$, $n = 136$, $P = 0.004$).

Complete incubation bouts.—We observed 260 complete incubation bouts. The mean length of a complete incubation bout at all nests was 12.73 ± 10.85 min. There were no differences in the mean length of complete incubation bouts for SY (13.79 ± 10.69 min; $n = 113$ bouts), ASY (12.47 ± 11.74 min; $n = 111$), or AHY (10.22 ± 7.94 min; $n = 36$) females when experimental and control nests were compared (all $P > 0.05$). There was no difference between the mean length of complete incubation bouts at experimental (13.61 ± 3.83 min; $n = 14$ nests) and control nests (12.43 ± 4.19 min; $n = 13$) with all females pooled together ($t = 0.76$, df = 25, $P = 0.45$). In addition, the mean incubation bout length was unaffected by day in the incubation period ($X^2 = 0.17$, df = 4, $P = 0.99$). Cloud cover, precipitation, wind-speed category, and air temperature inside and outside of the nest boxes were not significantly correlated with incubation bout length (all $P > 0.05$).

Reproductive performance.—SY and ASY females were pooled to examine the effect of the experimental treatment on reproductive performance because there were no differences between SY and ASY females in mean length of the incubation period, number of eggs hatched, number of nestlings alive on nestling day 12, number of fledglings produced, or the length of the nestling period. AHY females were not included in these analyses because sample sizes were too small to determine reliably the effects of feather removal on reproductive performance at the nests of AHY females; only one AHY female produced fledglings. The presence of feathers affected the reproductive performance of SY and ASY females. The incubation periods of females that nested in experimental nests were significantly longer than those of females that nested in control nests (Table 2). Females that nested in control nests produced

TABLE 3. Nestling growth ($\bar{x} \pm$ SD, with n in parentheses) to nestling day 12 at experimental (i.e. without feathers; $n = 9$ nests) and control (i.e. with feathers; $n = 10$ nests) nests. Wilcoxon's two-sample tests corrected for continuity used to compare means.

Measurement	Nests without feathers (nestlings)	Nests with feathers (nestlings)	Z
Tarsus length (mm)	11.44 ± 0.66 (28)	12.08 ± 1.04 (42)	−3.06**
Wing-chord length (mm)	34.86 ± 9.05 (28)	41.05 ± 6.29 (42)	−3.01**
Mass (g)	18.84 ± 3.64 (28)	20.44 ± 2.57 (42)	−2.32*

*, $P < 0.05$; **, $P < 0.01$.

TABLE 4. Nestling growth to nestling day 12 ($\bar{x} \pm$ SD) of nestlings reared by SY ($n = 7$), ASY ($n = 11$), and AHY ($n = 1$) females. Nested ANOVAs performed on ranks of tarsus length, wing-chord length, and mass.

	Nestlings reared by			*F*-value	
Measure	SY female ($n = 28$)	ASY female ($n = 42$)	AHY female ($n = 5$)	Female age within treatment (df = 4 and 65)	Nest box within treatment (df = 18 and 51)
Tarsus (mm)	11.64 ± 0.66	11.93 ± 1.09	11.76 ± 0.95	6.11***	6.20***
Wing-chord length (mm)	42.17 ± 3.24	35.67 ± 8.67	46.40 ± 7.23	7.40***	9.47***
Mass (g)	20.77 ± 1.76	19.03 ± 3.49	21.76 ± 3.10	3.11*	2.93**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

significantly more fledglings per nest than did females that nested in experimental nests (Table 2).

Effect on nestling growth.—On nestling day 12, nestlings that were reared in control nests (n = 10 nests; three control nests were abandoned during incubation) had significantly longer right tarsi and wing chords of the right wings, and weighed significantly more than nestlings reared in experimental nests (n = 9 nests; one experimental nest lost to predation and four abandoned during incubation; Table 3). ANOVAs that statistically nested swallows reared in different nest boxes or reared by females of different age classes within experimental or control groups showed that both nest box and female age class were significant sources of variation affecting nestling growth (Table 4).

Effect on ectoparasite abundance.—Most nestlings had no detectable ectoparasites; 11 of 28 (39%) nestlings in experimental nests and 15 of 42 (36%) nestlings in control nests had one or more ectoparasites. This relationship was unaffected by female age. Whether a nestling had one or more ectoparasites was independent of whether it was reared in an experimental or control nest (Fisher exact test, $P = 0.80$). Whether a brood was parasitized by ectoparasites was not independent of whether it was reared in an experimental or control nest ($P = 0.011$); nestlings in 4 of 9 (44%) experimental nests and all 10 (100%) control nests had parasites.

DISCUSSION

Nest architecture has the potential to influence reproductive performance in a variety of different ways. Clutch size may be positively correlated with the area of the nest-box floor in some hole-nesting species (e.g. Karlsson and Nilsson 1979, van Balen 1984, Gustafsson and Nilsson 1985, Slagsvold 1987). Nest insulation may influence reproductive performance by affecting the timing of breeding (O'Connor 1978) and the energetics 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), the risk of nestling hyperthermia (Mertens 1977b, Møller 1987, Lombardo 1994), and nestling growth (Winkler 1993). The population sizes of nest parasites that often adversely affect reproductive performance (Moss and Camin 1970, Brown and Brown 1986) may be correlated with nest architecture and material (Mason 1944, Møller 1987, Burtt et al. 1991, Clark 1991, Rogers et al. 1991, Winkler 1993).

During our experimental study, the presence of feathers lining the nest influenced the incubation behavior, nestling growth, and fledging success of Tree Swallows that nested in boxes in western Michigan. The insulative qualities of feathers are well known (Wainwright et al. 1976). Eggs in well-feathered nests cool slowly between bouts of incubation (Drent 1975), allowing incubating females to spend more time foraging (White and Kinney 1974). Poorly-insulated nests are energetically costly to incubating parents because parents must expend additional energy to warm eggs that cool during their absence. Thus, the ability of incubating parents to maintain optimum egg temperatures is influenced by nest insulation (Ricklefs 1974, White and Kinney 1974, Drent 1975). Central to the issue of egg-temperature regulation is incubation rhythm (i.e. the alternation between incubation sessions and recesses; von Haartman 1958, Drent 1975, Haftorn 1978). Individual variations in incubation rhythms reflect the en-

ergetic constraints on incubating individuals as they attempt to maintain eggs near the optimum temperatures for development (Ricklefs 1974).

The collecting of feathers that line Tree Swallow nests can be an important component of parental effort in these birds at least during some breeding seasons. Tree Swallows may fly many kilometers to collect white feathers to line their nests (Low 1933), indicating the extent to which they will invest energy to line their nests. Males add many of the feathers that line the nest, especially during egg laying and incubation (Sheppard 1977, Cohen 1985, Robertson et al. 1992, pers. obs.). Whittingham et al. (1994) incorrectly stated that male Tree Swallows do not assist their mates in nest building and, consequently, rejected the hypothesis that female Tree Swallows could gain assistance in nest building by copulating frequently with their mates. No one has yet examined the relationship between within-pair copulation rates and the number of feathers added to nests by male Tree Swallows. The feathers that line the nest cup are an important part of Tree Swallow nests because their presence influences incubation behavior and reproductive performance. Thus, feather collecting by male Tree Swallows is a form of paternal care and should be considered in theories about the evolution of parental care in this species. It is likely that this effect is due to both the insulative qualities of feathers (Wainwright et al. 1976) and their role as a barrier between nestlings and nest parasites (e.g. mites; Møller 1984, Cohen 1988, Winkler 1993).

The ability of incubating parents to maintain optimum egg temperatures is influenced by nest insulation (Ricklefs 1974, White and Kinney 1974, Drent 1975). Eggs that are not being incubated equilibrate with environmental temperatures at a rate that is dependent on the insulative qualities of the nest (Ricklefs 1974, White and Kinney 1974, Drent 1975). The temperature of developing eggs must be kept close to the optimum, 37°–39°C, for proper development (Gill 1994). Eggs in poorly-insulated nests reach ambient temperatures more rapidly than do eggs in well-insulated nests (Drent 1975). Parents with poorly-insulated nests must spend more time on eggs in order to maintain egg temperatures and, consequently, have less time available for foraging. For example, incubating Ringed Turtle-Doves (*Streptopelia risoria*) spent more time on cooled eggs than on warm eggs (Davis et al. 1984). Variations in incubation rhythms reflect the energetic constraints on incubating individuals as they attempt to maintain egg temperatures near the optimum (Ricklefs 1974).

However, for the Tree Swallows in our study, the presence or absence of feathers in the nest cup did not affect the amount of time females spent incubating eggs each hour or the mean length of complete incubation bouts. When ambient air temperatures were warm and aerial insects abundant (Williams 1961, Taylor 1963), female Tree Swallows spent more time off of their eggs in the air foraging than when ambient temperatures were cool and aerial insects were less abundant (Williams 1961, Taylor 1963). Early in the breeding season when the weather is often cold, females in poorly insulated nests would be to face two difficulties simultaneously. Because their nests are poorly insulated, their eggs would rapidly equilibrate with ambient temperatures, necessitating longer bouts of incubation to reach and maintain optimum temperatures, while at the same time bad weather would make foraging for aerial insects difficult (Williams 1961, Taylor 1963), thus requiring more time and energy. Female Tree Swallows commonly delay the start of incubation or interrupt incubation during cold snaps (Wedemeyer 1934, Kuerzi 1941, pers. obs.), suggesting that females reduce their parental effort when that effort puts them at energetic risk. Lombardo (1994) found that larger, well-insulated nests were advantageous early in the season in southeastern Michigan.

During our study, the presence of feathers lining the nest cup affected reproductive performance in three important ways that are discussed below. Each effect, taken alone or together, would provide intense selection pressure on Tree Swallows to collect feathers to line their nests. Competition for feathers is intense (Kuerzi 1941, Cohen 1985, Winkler 1993) and Tree Swallows go into a feather collecting frenzy when feathers are provided for them during nest building, egg laying, and incubation periods (Lombardo pers. obs.).

First, incubation periods were about one day longer at nests without feathers lining the cup (Table 2). Thus, females incubating in nests without feathers are at greater risk of predation because they are exposed to one more day of possible predation. During incubation, female Tree Swallows sit on their eggs at night.

Second, females that reared nestlings in nests without feathers produced fewer fledglings (Table 2). Interestingly, the influence of feathers on fledging success did not become apparent until the second half of the nestling period; there were no differences between experimental and control nests in the number of eggs that hatched or the number of nestlings that lived until nestling day 12 (Table 2). We did not visit nests between nestling days 12 and 20, so we were not able to determine the causes of mortality to those nestlings that died. However, on nestling day 12, the nestlings reared in experimental nests were smaller than the nestlings reared in control nests (Table 3). This result suggests that nestling size on nestling day 12 may be a predictor of the probability of nestling mortality over the remainder of the nestling period. Soon after nestling day 12, Tree Swallow nestlings attain their maximum mass and then gradually lose mass until fledging (Zach and Mayoh 1982). During mass loss, their feathers and wings grow (Zach and Mayoh 1982) as the nestlings' tissues lose water (Ricklefs 1968). If size on nestling day 12 is a predictor of nestling size at fledging, then nestlings reared in experimental nests (because they were smaller) had a lower probability of postfledging survival (O'Connor 1984), which would have depressed the reproductive success of females that reared nestlings in experimental nests even further.

During the course of Winkler's (1993) three-year study near Ithaca, New York, he found that feathers as nest lining had no effect on fledging success, but nestlings reared in nests with feathers fledged earlier. Lombardo (1994) found no correlation between the amount of nest feathering and fledging success in southeastern Michigan. The differences among Winkler's (1993), Lombardo's (1994), and the present study could reflect geographic differences in the importance of feathers as nest lining. However, it is more likely that the differences reflect the fact that we did not perform our experiments during enough breeding seasons to detect the true biological significance of feathers as nest lining in Tree Swallows. Furthermore, by ensuring that control nests had at least three complete layers of feather nest lining, the success of control nests in our study may have been elevated, or the variance in success at control nests reduced, thus increasing our chances of detecting a difference between experimental and control nests (Winkler pers. comm.). Taken together, the results from our three studies suggest that feathers lining the nest have a positive influence on Tree Swallow reproductive performance.

Third, nestlings reared in nests with feathers were significantly larger on nestling day 12 than those reared in nests without feathers (Table 4). Feathers lining the nest cup probably provide a thermal benefit to growing nestlings. Feathers may serve to prevent hypothermia in young nestlings before they become homeothermic (Winkler 1993). Tree Swallow nestlings do not become homeothermic until about nine days old (Dunn 1979, Marsh 1980). By providing extra insulation, feather nest linings may benefit growing nestlings by allowing more of their energy budgets to go to growth rather than to thermoregulation, thereby resulting in faster growth. By growing faster and shortening their time in the nest, nestlings may be able to reduce their risks of mortality due to ectoparasite loads, predation, and hyperthermia (O'Connor 1984, Winkler 1993). Fast-fledging nestlings also may benefit through increased time for independent foraging prior to molting and migrating south (Winkler, 1993). Nested ANOVAs revealed that female age class and the brood within which a nestling was reared both contributed significant sources of variation to nestling growth and suggest that future studies that directly examine the effects of these factors on nestling growth are warranted.

Differences between the feeding rates of parents with either control or experimental nests probably were not responsible for differences in nestling growth (Winkler 1993). We did not observe any differences between control and experimental nests in the mean number of parental feeding visits per hour or parental feeding visits per nestling per hour on nestling days 10 or 14 (Lombardo et al. unpubl. data).

Cohen (1988) argued that nest feathers were an antiparasite adaptation in Tree Swallows because the energy expended while competing for nest feathers outweighed their thermal benefits in the nest. In contrast to Winkler (1993), we found that feathers lining the nest had no effect on ectoparasite loads of individual nestlings. Likewise, 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. The lack of a relationship in our study between nest feathering and individual para-

site loads and our counterintuitive result that control nests were more likely to have one or more parasitized nestling are probably sample-size effects. We detected ectoparasites on relatively few of the nestlings in our study. Ectoparasite loads on nestlings vary from year to year (Lombardo unpubl. data), and it could be that the year of our study was one in which the role of nest feathers as barriers to ectoparasites was not important.

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