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OLD NEST MATERIAL IN NEST BOXES OF TREE SWALLOWS: EFFECTS ON NEST-SITE CHOICE AND NEST BUILDING

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ABSTRACT.—In natural cavities, old nest material accumulates with successive use, thereby reducing the size of the cavity, and allowing the numbers of certain haematophagous ectoparasites to increase. For this reason and because researchers studying birds breeding in nest boxes typically remove old nests from boxes, the results of such studies have been questioned. The accumulation of old nest material might affect nest-site selection and nest building by hole-nesting birds, so we tested this hypothesis by manipulating the presence and amount of old nest material in nest boxes of Tree Swallows (*Tachycineta bicolor*). Our experiment also allowed us to examine whether costs are incurred by females due to nest building in terms of their subsequent reproductive output. When a choice of boxes was available, swallows preferred empty and clean boxes, or those where the old material had been microwaved, over those with old, untouched material. Clean boxes and those with microwaved material had more space inside, so our experiments support two hypotheses: swallows avoid potentially high numbers of parasites in nests with old material; or they prefer large cavities. Empty boxes affected nest building. The mass and volume of nests built in clean boxes were greater than for nests built on old material. Females did not add more feathers to the nest lining in boxes with old material as compared with clean boxes. Correlation analyses suggested that females building large nests began egg laying earlier in both years. Otherwise, there were no associations between the sizes of nests built by females and subsequent reproductive output (e.g. clutch size) or nestling size (e.g. body-condition index). Our results show that the common habit of removing old nests from boxes can affect nest-site choice and nest-building behavior. Nest building does not influence reproductive output by Tree Swallows. *Received 16 May 1995, accepted 21 August 1995.*

NEST-SITE SELECTION is an important component of breeding behavior that may have ramifications for an individual's future reproductive effort and success. Nest-site characteristics, such as cavity orientation (Lumsden 1986, Rendell and Robertson 1994a) and cavity size (Karlsson and Nilsson 1977, Rendell and Robertson 1993), are extremely variable in natural populations, and have been shown to affect nest-site choice and reproduction for many species of cavity-nesting passerines. Because experimental manipulation of natural cavities may be impractical, or impossible, manipulation of the characteristics of nest boxes allows researchers to examine how extreme variations in nest-site qualities influence the breeding ecology of cavity nesters and, therefore, to gather insights into reproductive effort and the evolution of life histories.

Until Møller's (1989) critique, one cavity characteristic largely ignored was that of old nest material. Because researchers typically remove old nest material from nest boxes after each breeding season, Møller stated that individuals that nest in boxes experience unrealistically beneficial breeding conditions. In natural cavities, old nest material accumulates with successive use, and so do the numbers of some types of haematophagous ectoparasites (e.g. bird fleas; unpubl. manuscript). Studies have shown that many types of parasites can reduce the reproductive success of cavity nesters (e.g. Moss and Camin 1970, Richner et al. 1993, Winkler 1993). Many important long-term studies of life history have been done using cavity-nesting birds in nest-box populations, so it is important to assess the possible effects of old material on the breeding ecology of cavity nesters, and to consider whether or not such studies could or should be reinterpreted.

Cavity-nesting birds may frequently have a choice of nest sites in which to breed, perhaps because their territory includes two or more

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cavities (e.g. Rendell and Robertson 1994b). Given that parasites can reduce reproductive success, and that some parasites are more numerous in old nests, cavity-nesting birds may discriminate between high and low infestations of parasites, and so avoid cavities with old material. Some birds that reuse nests—such as Barn Swallows (*Hirundo rustica*; e.g. Barclay 1988), Cliff Swallows (*H. pyrrhonota*; e.g. Brown and Brown 1986), and Great Tits (*Parus major*; Oppliger et al. 1994)—can discriminate between nest sites with and without high numbers of parasites, and they avoid the former.

The accumulation of old material shrinks cavity size. For some cavity-nesting birds, clutch size is positively associated with cavity size (e.g. Rendell and Robertson 1993, Rendell and Verbeek 1996), so these birds may prefer cavities with less old material.

Benefits of energy savings in using nests with old material may outweigh potential costs of nest reuse due to ectoparasitism and smaller cavity size. By reusing an old cavity, cavity nesters might devote their energies to foraging and egg production. Nest building has long been considered energetically costly. However, whether nest building is costly in terms of reproductive effort within a breeding season, or between seasons, remains unknown. To date, no conclusive evidence for a reproductive cost due to nest building exists (Winkler and Wilkinson 1988, Conrad and Robertson 1993).

Alternatively, old material may not influence nest-site selection if, for example, the birds clean out old nests (e.g. House Wrens, *Troglodytes aedon*; Thompson and Neill 1991, Johnson 1996), or if they construct new nests of plant materials (e.g. European Starlings, *Sturnus vulgaris*; Clark 1991) and animal materials (e.g. Tree Swallows, *Tachycineta bicolor*; Winkler 1993) that deter parasitism.

Here, we present the results of experiments on how old nest material influences box selection and nest building by Tree Swallows breeding in British Columbia. Because we also recorded the reproductive success and nestling size of Tree Swallows during this study (Rendell and Verbeek 1996), we will examine whether nest building was costly to females in terms of their current reproductive output. In contrast to studies performed simultaneously with ours (e.g. Oppliger et al. 1994), we manipulated parasite loads in boxes indirectly, by experimenting with the presence and abundance of old nest material, to test the assumption that parasites are more numerous in boxes with old nests (cf. Møller 1989). We found that bird fleas were more numerous in boxes with old nest material compared to clean boxes, whereas blow flies and fowl mites were equally numerous in all box types (unpubl. manuscript).

METHODS

Species studied.—Tree Swallows are socially monogamous, single-brooded insectivores that have been studied extensively in box and cavity populations (Robertson et al. 1992). Females build the nest, mainly using dead grasses. Males and females collect feathers to line the cup. Females apparently time egg laying for the middle of May to take advantage of favorable environmental conditions, and possibly to benefit from synchronous nesting (Stutchbury and Robertson 1987a, 1988). Tree Swallows at our study site are hosts to three types of haematophagous ectoparasites: blow flies (*Protocalliphora sialia*), northern fowl mites (*Ornithonyssus sylviarum*), and bird fleas (*Ceratophyllus idius*), which will be described in greater detail in a forthcoming manuscript.

Study site and box types.—We conducted this research in marsh habitat at the Creston Valley Wildlife Management Area (CVWMA), British Columbia (49°05'N, 116°35'W), in 1991 and 1992. Tree Swallows had bred in about 160 plywood and wood boxes on dikes at CVWMA for a decade. Our boxes were mounted 1 m off the ground on wooden posts with metal predator guards. All the boxes were within 40 m of water. In 1991 we arranged the boxes in pairs for a box-preference experiment. In 1992 the boxes were redistributed; 125 boxes of two types were arranged singly and alternately, 30 to 40 m apart, along dikes. Tree Swallows occupied all 79 territories in 1991, and 112 of 125 (90%) boxes in 1992.

We used four types of boxes during 1991 and 1992: (*C*) clean; (*S*) sham (1991 only); (*CI*) clean with inserts (1992 only; see below); and (*O*) old boxes. In *C* boxes, the old nests were removed and the inside was swept with a wire brush to loosen all duff and droppings. Care was taken to clean in the cracks of boxes, where possible, to kill or flush out hidden parasites. *S* boxes received the same treatment as *C* boxes except that, after cleaning, one microwaved nest was inserted. We collected 50 old nests from boxes at CVWMA, and microwaved each one in a Look cooking bag for 5 min on high power in a Toshiba oven. Old nest material was available at CVWMA because the boxes were not cleaned after the 1990 breeding season. To determine the effectiveness of this procedure, we sifted 3 of the 50 nests (each of which had living arthropods before microwaving) after microwaving. All of the arthropods in these nests were dead, so we are confident that this procedure killed parasites in all

50 nests. *O* boxes were not manipulated in any way; the old nest material was left in place and the boxes were not cleaned. Nest material used at both *S* and *O* boxes showed evidence of occupancy the previous year (e.g. dead nestlings and bird droppings). Therefore, any parasites in these boxes presumably would have had access to hosts previously, and could have increased in number.

Nest-box preference experiment.—We performed a box-preference experiment using *C*, *S*, and *O* boxes in 1991. The boxes were distributed in pairs with each box in a pair 3 m apart, and pairs 40 m apart. We called a pair of boxes a territory. This design provided a choice of boxes to each pair of swallows. The boxes were paired as follows: *C* with *O* on 29 territories; *C* with *S* on 25 territories; and *S* with *O* on 25 territories. We arranged the three types of territories sequentially throughout the marsh: $C \times O1$, $C \times S1$, $S \times O1$, $C \times O2$, . . . , etc. All boxes were in place by 25 March, before the swallows began settling. We determined box preference according to the box in which a female built her nest and laid her clutch. At one territory a pair of Black-capped Chickadees (*Parus atricapillus*) already occupied one of the boxes before Tree Swallows settled at the other box, so this territory was dropped from the analysis.

Nest-building experiment.—We conducted an experiment with box inserts in 1992 to examine how cavity size influenced the size of new nests. In 15 randomly chosen *C* boxes (hereafter designated *CI*), compact styrofoam and a plywood floor overlay were inserted to fill the bottom 8 cm of each box. Therefore, *CI* boxes were clean, but they simulated the smaller cavity of boxes with old nest material. The depth of the inserts approximated the mean depth of old nest material in *O* boxes in 1992 ($\bar{x} = 7.4 \pm$ SE of 0.3 cm, $n = 58$). Two *CI* boxes were not used by Tree Swallows.

We recorded the mass (g) of all new nests built once the nest cups were formed, but yet unlined. New and old nests were distinguished easily, and nest structures were relatively dry when weighed. We weighed nests in a ZIPLOC bag with a Pesola scale (50–300 g), and then replaced them in boxes intact. Many nests built on top of old nest material were very light and fragile, so we had to estimate their mass (i.e. 1 or 5 g) because handling would have destroyed them. The estimates were based on the masses of three nests that were weighed despite their small size.

We repeatedly measured the depth (cm) of new and old nest structures in each box before the settlement of pairs in boxes, until the new nests were completed. Using the dimensions of each box and the depth of new and old nests in a box, we calculated the volume of new and old nest structures (cm^3), and the cavity (cm^3) above the floor or nest material before settlement and before egg laying.

Feathers.—We collected nests after a breeding attempt failed or the young fledged. The number of feathers collected for new nests was determined by counting the rachises in sifted nests. Feathers that were obviously part of an old nest structure were not counted. Feather counts were made for 30 nests in 1991 ($n_C = 18$, $n_S = 8$, $n_O = 4$), and 100 nests in 1992 ($n_C = 34$, $n_{CI} = 13$, $n_O = 53$).

Cost of nest building.—Elsewhere (Rendell and Verbeek 1996), we describe that, when comparing the reproductive success of birds using the four box types, we switched nests under females in an attempt to control for possible covariation between the phenotype of females, their reproductive success, and the box type they chose. This procedure was done after nest sites were chosen and new nests were built, but before egg laying.

For the purposes of analyzing reproductive output after nest building in our study, we excluded females involved in nest switches, because the new microenvironment of their altered nest and box could have influenced breeding. We also excluded females whose approximate age was unknown. Therefore, our analysis of cost of nest building is based on the reproductive output of 34 females in 1991, and 85 in 1992.

Banding and female age.—We captured females by hand, in mist nets, and using box traps (Stutchbury and Robertson 1986). They received Canadian Wildlife Service (CWS) aluminum bands and were individually identified with nontoxic acrylic paints at positions on the wing and tail. Females were sexed and aged according to Hussell (1983) and Stutchbury and Robertson (1987b). They were aged as second-year (SY) and after-second-year (ASY) birds in 1991, but recaptures in 1992 allowed us to divide female ages into three classes: SY, ASY (including third year), and after-third-year birds (ATY, including fourth year).

Breeding and nestling size.—We recorded breeding phenology and reproductive success during regular nest checks (i.e. conducted each day during egg laying, hatching, and fledging; every three days during incubation and nestling periods). Variables recorded included: dates of first egg, hatching, and fledging; duration of incubation and nestling periods; number of eggs, hatchlings, fledglings, and dead young; and percentages of hatchlings/eggs laid, fledglings/hatchlings, and fledglings/eggs laid. The first-hatching day was nestling day (ND) 1. First-fledging day was the date when the first nestling left the nest. Incubation period was the number of days from when the last egg was laid to first hatching, and nestling period was the number of days between ND 1 and the day the last nestling fledged or died.

We banded nestlings with CWS bands on ND 15. This day was chosen because: (1) young have attained peak structural size, and they are close to peak mass (Zach and Mayoh 1982); and (2) the first young may fledge from a nest on ND 16 (Rendell and Verbeek 1996). During banding we measured the flattened wing length (i.e. from "wrist" to tip of ninth primary, mm), ninth primary length (i.e. from insertion point of

TABLE 1. Box types chosen by Tree Swallows at paired-box territories in 1991. Box types are: (*C*) clean; (*S*) sham; and (*O*) old. *P*-values are binomial probabilities, and are the same for box type and size tests.

		Box chosen			
Territory	n	C	S	O	P
$C \times S$	25[a]	18	6	—	0.011
$C \times O$	29	22	—	7	0.004
$S \times O$	25	—	19	6	0.007

[a] One territory was excluded because another species occupied one box prior to settlement by Tree Swallows.

TABLE 2. Mass (g) and volume (cm^3) of new nest material gathered by female Tree Swallows. Values are $\bar{x}$ ± SE (*n* nests).[a]

Box type	Mass	Volume
	1991	
Clean	24.2 ± 1.8^{A} (40)	827.1 ± 34.0^{A} (39)
Sham	4.8 ± 1.3^{B} (25)	307.7 ± 54.2^{B} (22)
Old	5.9 ± 1.4^{B} (13)	428.7 ± 75.4^{B} (12)
	1992	
Clean	26.3 ± 1.3^{A} (40)	712.6 ± 25.9^{A} (39)
Clean(*I*)	16.4 ± 1.4^{B} (13)	581.6 ± 27.5^{B} (14)
Old	6.3 ± 0.7^{C} (58)	287.2 ± 24.9^{C} (58)

[a] $P < 0.001$ for both parameters within both years (Kruskal-Wallis tests, two-tailed, df = 2). Values with the same capital letter are not different ($P < 0.05$, multiple-comparison method; Siegel and Castellan 1988).

primary in manus to tip of primary, mm), and mass (g) of nestlings. For a structural measure of size of young, we subtracted ninth-primary length from wing length to get manus length (Pettingill 1985). For an index of body condition for individual nestlings we used the following equation: $\text{mass}/(\text{manus})^3$ (cf. Slagsvold and Lifjeld 1988).

Statistical analysis.—To minimize the possible effects of season (Stutchbury and Robertson 1988, Lombardo 1994), we analyzed only nests in which the first egg was laid before 1 June. Also, renesting attempts by females whose first attempt had failed were not included in any analyses. The nest-building data were not combined between years due to differences in experimental protocol. The data on reproductive success were not combined between years because of the experimental differences, and because several measures of reproductive success and nestling size were significantly different between years (Rendell and Verbeek 1996). We combined data for all female age classes because there were no significant differences in reproductive success or nestling size among them within boxes and years (Rendell 1992), and because female age-class distributions did not differ between box types, before or after nest switches were made (see below). For analysis, within-nest means were calculated for all nestling size variables. We used nonparametric statistics (SAS Institute 1985, Siegel and Castellan 1988), and a significance level α of 0.05. After correlation analyses, we applied sequential Bonferroni correction tests (Rice 1989) to determine tablewide significance levels and minimize the likelihood of committing a type-I error. Where sample sizes vary between tests, this is due to missing values.

RESULTS

Nest-box preference.—Nest-box choice was nonrandom for all three paired-box combinations (Table 1). *C* boxes were preferred over both *S* and *O* boxes, and *S* boxes were preferred over *O* boxes. These results could have been biased because of a variable that we did not control (i.e. the difference in cavity size between boxes). Both *S* and *O* boxes had old nest material, so their cavity sizes were always smaller than *C* boxes. On 17 territories with both *S* and *O* boxes, the *S* box had less old nest material and, therefore, larger cavity size than the *O* box. On five territories with *S* and *O* boxes this was reversed, and on three territories the cavity sizes were the same between boxes. For each of the three types of territories, we analyzed box preference with respect to cavity size of each box. The swallows more often chose the box in a pair with the larger cavity (see binomial probabilities in Table 1).

Female age, and presumably experience, did not affect the choice of nest sites. The numbers of ASY and SY females that chose *C* versus *S* and *O* boxes were not significantly different (2 × 2 test, Pearson $\chi^2 = 0.29$, df = 1, $P = 0.59$). To meet all the requirements for a valid chi-square test (Siegel and Castellan 1988), we combined the numbers of ASY and SY females in *S* and *O* boxes, so the test was between the distributions of ages of females in clean boxes versus those in boxes with old material.

Nest building.—Box type significantly influenced the volume and mass of new nest material brought to nests. Females using *C* boxes built significantly larger and heavier nests than birds using *S* or *O* boxes in 1991 (Table 2). Nests built in *C* boxes in 1992 were significantly larger and heavier than those built in *CI* boxes, and new nests in *CI* boxes were significantly larger and heavier than those in *O* boxes. The mass and volume of new nests built by females were sig-

TABLE 3. Mass (g) and volume (cm^3) of new nests built by older and younger female Tree Swallows, irrespective of box type. Values are $\bar{x}$ ± SE (n females). No significant differences found between female age classes for mass or volume within years (Mann-Whitney and Kruskal-Wallis tests, all $P > 0.59$).

Female age[a]	Mass	Volume
	1991	
SY	16.2 ± 3.6 (10)	597.8 ± 93.8 (10)
ASY	14.9 ± 1.6 (63)	601.9 ± 45.4 (57)
	1992	
SY	13.7 ± 2.6 (23)	451.4 ± 58.9 (22)
ASY	14.0 ± 1.3 (54)	483.3 ± 33.6 (54)
ATY	15.9 ± 2.5 (30)	464.4 ± 52.1 (31)

[a] Ages are: (SY) second-year; (ASY) after-second year, including third year; and (ATY) after-third year, including fourth year.

TABLE 4. Volume (cm^3) of boxes above the nest, after the completion of new nests by female Tree Swallows. Values are $\bar{x}$ ± SE (n nests).[a]

Box type	Volume
	1991
Clean	1,763 ± 37^{A} (37)
Sham	1,539 ± 62^{B} (19)
Old	1,551 ± 67^{B} (12)
	1992
Clean	1,888 ± 33^{A} (36)
Clean(*I*)	1,205 ± 40^{B} (13)
Old	1,515 ± 36^{C} (56)

[a] $P < 0.005$ for both years (Kruskal-Wallis tests, two-tailed, df = 2). Values with the same capital letter are not different ($P < 0.05$, multiple-comparison method; Siegel and Castellan 1988).

nificantly positively correlated with cavity size at settlement (mass in 1991, Spearman rank-order correlations, $\rho = 0.76$, $n = 72$; mass in 1992, $\rho = 0.72$, $n = 111$; volume in 1991, $\rho = 0.77$, $n = 72$; volume in 1992, $\rho = 0.67$, $n = 111$; all $P < 0.001$). Many females building in boxes that contained old material brought less than 5 g of grass to the nest (1991, 16 of 25 *S* boxes [64%], 5 of 13 *O* boxes [38.4%]; 1992, 38 of 58 *O* boxes [65.5%]). These individuals merely lined existing material with a thin layer of grass and then added feathers.

Female age did not affect nest mass (1991, Mann-Whitney [M-W] U-test, $U = 0.53$, $P = 0.59$; 1992, Kruskal-Wallis [K-W] test, $H = 0.44$, df = 2, two-tailed, $P = 0.80$) or volume (1991, $U = 0.12$, $P = 0.90$; 1992, $H = 0.59$, df = 2, two-tailed, $P = 0.74$) in either year, when all boxes were combined (Table 3).

After new nests were completed, cavity size above the nest material was still significantly greater in *C* boxes than in *S* and *O* boxes in 1991 (K-W test, $H = 12.0$, df = 2, $P < 0.005$), and greater in *C* boxes than in *CI* and *O* boxes in 1992 ($H = 51.0$, df = 2, $P < 0.001$; Table 4). Remaining cavity sizes were not different between *S* and *O* boxes in 1991, but were significantly greater in *O* boxes compared to *CI* boxes in 1992 (multiple-comparison method, $P < 0.05$; Siegel and Castellan 1988).

Feathers.—Neither box type (1991, K-W test, $H = 3.2$, df = 2, $P = 0.21$; 1992, $H = 3.0$, df = 2, $P = 0.23$; Table 5) nor female age (1991, M-W test, $U = 0.2$, $P = 0.84$; 1992, K-W test, $H = 2.6$, df = 2, $P = 0.28$) affected the numbers of feathers incorporated into new nests by pairs in either year.

Cost of nest building.—First, we reanalyzed our data to ensure that the aspects of the ecology of the subset of females used in the cost analysis reflected those of all the females combined. There was a significant positive correlation between cavity size at settlement, and nest mass (1991, $\rho = 0.71$, $n = 31$; 1992, $\rho = 0.78$, $n = 84$; both years, $P < 0.001$) and nest volume (1991, $\rho = 0.74$, $n = 31$; 1992, $\rho = 0.71$, $n = 84$; both years, $P < 0.001$) of new nests that females built. The masses and volumes of nests built by older and younger females were not different (all $P \geq 0.60$). In both years, the age distributions of females using the three box types were not different (all $P \geq 0.83$).

First-egg date was negatively correlated with the mass of new nests built by females in 1992

TABLE 5. Numbers of feathers incorporated into new nests by Tree Swallows. Values are $\bar{x}$ ± SE (n nests; range). No significant differences found between box types for numbers of feathers within years (Kruskal-Wallis tests, all $P > 0.21$).

Box type	Number of feathers
	1991
Clean	138 ± 8 (18; 84-186)
Sham	157 ± 23 (8; 73-286)
Old	241 ± 50 (4; 95-318)
	1992
Clean	139 ± 9 (34; 62-317)
Clean(*I*)	116 ± 11 (13; 61-183)
Old	118 ± 7 (53; 34-278)

TABLE 6. Correlations between selected variables of nesting phenology, reproductive output, and nestling size with the mass (g) and volume (cm^3) of new nests built by female Tree Swallows. Values are Spearman's rank-order correlation coefficients, ρ (n females).

Variable	Mass	Volume
	1991	
First egg date	−0.13 (34)	−0.34 (31)
Incubation period (days)	−0.40 (30)	−0.36 (29)
Nestling period (days)	0.22 (28)	0.25 (27)
Clutch size	0.11 (33)	0.26 (31)
Number fledglings/clutch size	0.06 (30)	−0.04 (29)
Nestling condition index[a]	0.07 (29)	0.03 (28)
	1992	
First egg date	−0.31* (83)	−0.27 (84)
Incubation period (days)	−0.08 (80)	−0.02 (81)
Nestling period (days)	−0.07 (69)	−0.03 (69)
Clutch size	0.15 (81)	0.07 (82)
Number fledglings/clutch size	0.02 (80)	0.11 (81)
Nestling condition index	0.01 (68)	−0.06 (68)

[a] Index = mass/(manus)^3; see Methods for more details.

* $P = 0.004$; table-wide corrected $\alpha = 0.008$ after sequential Bonferroni correction (cf. Rice 1989).

(Table 6). Otherwise, there were no significant associations between nesting phenology, subsequent reproductive output, or nestling size on ND 15 in either year (Table 6; 1991, all $P \geq 0.03$; 1992, all $P \geq 0.01$; corrected $\alpha = 0.008$ after sequential Bonferroni corrections; cf. Rice 1989). Further, we performed partial correlations of clutch size with nest mass and nest volume, when controlling for female age, first-egg date, and cavity size at settlement. We found no significant correlations between these variables (1991, all $P \geq 0.14$; 1992, all $P \geq 0.35$).

DISCUSSION

Tree Swallows clearly preferred clean boxes over those with old nest material, although our experiment failed to determine if they were avoiding the higher ectoparasite populations in boxes with old material (unpubl. manuscript), or if they were simply looking for the largest available cavity. We found a significant positive correlation between cavity size and clutch size in each year when we combined the clutches from all box types (Rendell and Verbeek 1996). Also, Rendell and Robertson (1993 and references therein) showed that Tree Swallows, like other species of secondary cavity nesters, prefer to nest in large cavities when a choice is available, and that females lay larger clutches in larger cavities. However, it is possible that, like other hirundines (e.g. Cliff Swallows [Brown and Brown 1986, Emlen 1986, Chapman and George 1991, Loye and Carroll 1991], Barn Swallows [Møller 1987, 1990, Barclay 1988, see also Shields 1984, Shields and Crook 1987]) and Great Tits (Christe et al. 1994, Oppliger et al. 1994), Tree Swallows have evolved the ability to discriminate between nests with high and low parasite populations. On territories with sham and old boxes where cavity sizes were similar, Tree Swallows avoided boxes with old, unmanipulated nests. The cue that enabled Tree Swallows to distinguish between microwaved and unmanipulated old nests may have been the movement of adult fleas, both in the existing nest structure or on the outside of a box. W.B.R. once observed tens of adult fleas surrounding a box entrance in early spring, presumably waiting for a host. Analogous to observations of cyclic colony use by colonially nesting hirundines (e.g. Loye and Carroll 1991), if some hole nesters in the wild avoid cavities because of high parasite loads, this could be an explanation why many studies investigating cavity availability for secondary hole nesters have found numerous, unoccupied cavities in natural populations (e.g. van Balen et al. 1982, Brush 1983, Ingold and Ingold 1984, Peterson and Gauthier 1985, Rendell and Robertson 1989, Waters et al. 1990).

Contrary to Møller's (1989) hypothesis, studies have shown that some species of hole-nesting birds may choose cavities independent of the presence or absence of old nest material (e.g. House Wrens; Thompson and Neill 1991, Johnson 1996), or actually prefer cavities with old nests (e.g. Eastern Bluebirds [*Sialia sialis*], Davis et al. 1994; Pied Flycatchers [*Ficedula hypoleuca*], Mappes et al. 1994; see also Jackson and Tate [1974] for Purple Martins [*Progne subis*]). Christe et al. (1994) suggested that parasite populations in the cavities used in such studies may have been so low as to be negligible, and so did not affect cavity choice, but we suggest four additional hypotheses may account for these unexpected results. As Mappes et al. (1994) showed, hole nesters may choose boxes with old nests when large parasite populations are in "clean" boxes. Also, generic differences in nest-building behavior may preclude the need for individuals to locate clean cavities. To some hole-nesting species—such as House Wrens, which remove old material from cavities (e.g. Johnson 1996), and European Starlings, which line their nests with specific plant species that deter parasites (e.g. Clark 1991)—the presence or absence of old nests may be immaterial. Further, cavities with old nests showing evidence (e.g. nestling feces) of having been used successfully in the past may be judged as suitable for use again (Thompson and Neill 1991, Johnson 1996). Finally, by choosing to use cavities with old nest material, some species may be avoiding interspecific competition. For example, Tree Swallows prefer cleaner and/or larger cavities, House Wrens show no apparent preference, and Eastern Bluebirds prefer cavities with old material. Interestingly, all three species compete directly and intensively for cavities (Rendell and Robertson 1990).

Tree Swallows showed great variability in the size of the nests they built, a variable influenced by box type and cavity size. Correlations showed that nest size increased with cavity size. Lombardo (1994) found that Tree Swallows in southeastern Michigan also built bigger nests (e.g. by nest volume) in bigger boxes. Pitts (1988) observed the same behavior in Eastern Bluebirds. Similar to Lombardo (1994), we found no effect of female age on the sizes of new nests built in boxes. The larger nests observed in clean or larger boxes may be needed to ensure a stable platform for the nest cup and eggs, to provide adequate insulation, or to enable young and adults to leave the box more easily.

It is likely that the observed size of some of the nests in our study, as well as other studies of hole nesters, are an artifact of the size of boxes used by researchers; on average, the volumes of nest boxes provided by researchers are greater than those of natural cavities (e.g. Robertson and Rendell 1990). Apparently, however, nest building is not costly to female Tree Swallows in terms of their subsequent reproductive output (see also Lombardo 1994). Conrad and Robertson (1993) found a similar result for an open-nester, Eastern Phoebes (*Sayornis phoebe*). For many Tree Swallows this may be, in part, because they arrive on their breeding grounds up to one and a half months before the median first-egg date of the population. For example, in 1991, the first Tree Swallows arrived in our population on 17 March (W.B.R. pers. obs.), yet the mean first-egg date that year was not until 8 May (Rendell and Verbeek 1996). Stutchbury and Robertson (1987a) experimentally delayed settlement at nest boxes by female Tree Swallows in southeastern Ontario. They reported a significant positive association between settlement date at nest sites and the date of the initiation of nest building, and a significant negative association between settlement date and the interval of days until egg laying. So, by returning early in the spring, females may locate and secure clean large cavities, and build large nests over an extended period of time, thus allowing them time to forage in preparation for egg laying and incubation, despite any extra effort expended during nest building. As is the case in our study, possible early arrival and the building of large nests may be associated with slightly advanced first egg dates (Table 6), but in general, most female Tree Swallows time egg laying for the middle of May (Stutchbury and Robertson 1987a, 1988).

We caution that our conclusion that there is no reproductive cost to nest building is based solely on correlations. A better test of the cost of nest-building hypothesis in hole-nesting birds would be to assess clutch size and reproductive output of birds that arrive late on their breeding grounds, but must build a large nest in the short period of time that precedes the mean first-egg date of the population. Under these circumstances, if there is a reproductive cost to nest building, we predict a significant reduction in clutch size and reproductive output.

Feathers serve an important thermoregulatory function by insulating eggs and nestlings (Capreol 1983, Møller 1984). Winkler (1993) manipulated the number of feathers in nest cups of Tree Swallows and showed that nestlings with more feathers in their nest cups were larger and had fewer parasites (i.e. fowl mites, lice), indicating that feathers may deter parasite feeding. In our study, bird fleas were more numerous in nests with old material and, based on Winkler's results, one might expect that birds should have incorporated more feathers into these nests. However, this was not observed and, furthermore, nestling health was not affected (Rendell and Verbeek 1996); thus, our results do not corroborate those in Winkler (1993). Likewise, Lombardo (1994) found no association between the numbers of feathers in nests of Tree Swallows and hatching and fledging success. Capreol (1983) also found that feathers did not deter the blow fly *Protocalliphora sialia* from feeding on nestling Tree Swallows. Tree Swallows add feathers to the cup lining until hatching, but not after, so it is possible that the birds in our study did not recognize the higher flea loads in boxes with old material until after the young had hatched, or that flea numbers increased as the nestling stage progressed. However, we dismiss these two explanations because Tree Swallows apparently discriminated between parasitized (O) and relatively unparasitized (S) nests during the box-preference experiment, and because there was no significant effect of season on the numbers of the three types of parasites found in boxes in this study (unpubl. manuscript). Our results differ from those of Winkler (1993) in another way. He found a negative correlation between the duration of the nestling period and the number of feathers in a nest at hatching in each year of a three-year study (significant in one of the three years), suggesting that more feathers in the nest cup enable young to grow faster and fledge earlier. We found no association between the number of feathers in a nest and the duration of the nestling period in 1991 (Spearman rank-order correlation, $\rho = 0.03$, $n = 29$, $P = 0.89$), and a significant positive correlation between these variables in 1992 ($\rho = 0.29$, $n = 84$, $P = 0.007$). We think that nestling periods were longer for young in nests with more feathers in 1992 because the feathers contributed to the heat stress experienced by nestlings during a heat wave in June of that year, and this heat stress likely slowed growth rates. The mean temperature in June 1992 was significantly warmer by almost 6°C than that for June 1991 (unpubl. manuscript); temperatures exceeded 30°C for nine consecutive days, and most of the incidents of entire brood death in 1992 occurred during that period (Rendell and Verbeek 1996). Feathers can decrease the rate of heat loss in nests (Capreol 1983), so during warm periods more feathers in a nest may be detrimental because cavity temperatures could be kept dangerously high. In support of this hypothesis, Lombardo (1994) found evidence that well-insulated nests (i.e. those with a greater volume of nest material) decreased fledging success for Tree Swallows late in the breeding season, presumably when high nest temperatures led to hyperthermia in nestlings.

The results of our study lend some support to Møller's (1989) critique of nest-box studies, and the habit of removing old nest material from nest boxes. Old nest material in nest boxes influences nest-site choice and nest-building behavior in Tree Swallows. If nest building is periodically costly for individual hole nesters, measured by their reproductive output, removing old nests from nest boxes may affect the quantitative results of long-term studies of lifetime reproduction by hole-nesting birds.

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