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OLD NEST MATERIAL IN NESTBOXES OF TREE SWALLOWS: EFFECTS ON REPRODUCTIVE SUCCESS[1]

WALLACE B. RENDELL[2] AND NICOLAAS A. M. VERBEEK
Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

Abstract. Researchers studying hole-nesting birds breeding in nestboxes typically remove old nests from boxes. In natural cavities, old nest material accumulates with successive use. Here, we report on a two-year experiment concerned with the effects of the accumulation of used nest material in nestboxes on the reproductive success of Tree Swallows (*Tachycineta bicolor*). Tree Swallows nested in clean boxes, boxes with old, unmanipulated material, and in boxes with old nests that had been microwaved to kill parasites inside. Bird fleas (*Ceratophyllus idius*) were more numerous in boxes with old nest material compared to clean boxes in both years. Reproductive output and nestling size were significantly reduced in the second year of the study, possibly because of higher numbers of bird fleas in two box-types that year. However, all instances of entire brood loss that year occurred during two periods of extreme weather, so we cannot distinguish between the possible effects of parasites and climate. In one year, the swallows nested later in boxes with old material. Otherwise, nesting phenology, reproductive output, and nestling size were not different between pairs using boxes with and without old material in either year. In both years, there was a significant, positive correlation between clutch size and cavity size. Contrary to some recent studies, there were no significant associations between the numbers of fowl mites (*Ornithonyssus sylviarum*), bird fleas, or blowflies (*Protocalliphora sialia*) per nestling, and any measures of reproductive output or nestling size in either year. We discuss our results in light of a recent critique of studies of birds breeding in nestboxes.

Key words: Old nests; nestboxes; ectoparasites; reproductive success; Tree Swallows; Tachycineta bicolor.

INTRODUCTION

Within the last decade, ecologists have recommended that the results from nestbox studies of birds be interpreted with caution because several characteristics of boxes and box populations may be different from those of natural cavities and cavity populations (van Balen et al. 1982; Korpimäki 1984; Nilsson 1984; Møller 1989, 1992; Robertson and Rendell 1990). Møller (1989) pointed out a novel difference between boxes and tree cavities. Researchers typically remove old nest material from boxes after each breeding season, whereas old material accumulates in tree cavities. Møller hypothesized that this introduces an experimental artifact to box studies that calls the validity of results into question. He claimed that by removing old material from boxes researchers reduce the numbers of hematophagous ectoparasites, and he noted that parasites may have a significant effect on reproductive output and nestling growth. He concluded that investigations into the effects of old nest material and parasites on the ecology of hole-nesting birds were necessary to clarify the results of previous research. These criticisms are important because much of our knowledge and understanding of the evolution of avian life-histories and ecology is based on observations and experiments from long-term studies of hole-nesting birds breeding in boxes.

Møller (1989) prompted a rebuttal in defense of box studies by Koenig et al. (1992) based on philosophical and practical arguments, and some subsequent empirical work has both supported (e.g., Richner et al. 1993) and disagreed (e.g., Johnson and Albrecht 1993) with some of the assumptions and predictions of Møller's critique. We (Rendell and Verbeek, unpubl.) have shown that some types of hematophagous parasites (i.e., bird fleas, *Ceratophyllus idius*) of Tree Swallows (*Tachycineta bicolor*) are more numerous in nestboxes with old nest material, confirming a crucial

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[2] Present address: Dept. Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

assumption in Møller (1989). We have further shown (Rendell and Verbeek, in press) that nestbox choice and nest building may both be affected by old material; birds may avoid boxes with old nests because of higher associated numbers of parasites, or smaller average cavity size, and females build bigger nests in clean boxes. Here, we present the results of experiments on how old nest material influences reproductive success for Tree Swallows breeding in British Columbia. Tree Swallows are socially monogamous, single-brooded insectivores that have been studied extensively in nestbox populations (Robertson et al. 1992). Unlike other species of hole-nesters (e.g., House Wren, *Troglodytes aedon,* Johnson 1996), they do not remove old nest material from cavities, but simply build over an existing nest. At our study site they are hosts to three types of hematophagous parasites, including bird fleas, blow flies (*Protocalliphora sialia*), and Northern fowl mites (*Ornithonyssus sylviarum*), all of which we describe in detail elsewhere (Rendell and Verbeek, unpubl.).

METHODS

STUDY SITE

Our study was conducted in marsh habitat at the Creston Valley Wildlife Management Area (CVWMA), British Columbia, Canada (49°05′N, 116°35′W), in 1991 and 1992. A large population of Tree Swallows has bred there in nestboxes for a decade. Nestboxes were mounted on posts with predator guards, within 40 m of water.

Four types of boxes were used: clean (C), sham (S, 1991 only), clean with inserts (CI, 1992 only), and old (O) boxes. *C boxes* were cleaned by removing old nests and scraping each box thoroughly with a wire brush. *S boxes* were treated similarly, after which we inserted a microwaved nest into each of them. To microwave nests, we collected used nests from boxes at CVWMA and microwaved each separately in a plastic cooking bag for 5 min on higher power. Each nest was then sealed separately in a clean ziploc bag. Old nests were available because the boxes were not cleaned after the 1990 breeding season. Three of the 50 collected old nests were sifted after microwaving, and all the arthropods in these nests were dead. *O boxes* were not manipulated in any way; the old nest material was left in place. Nest material used at both S and O boxes showed evidence of occupancy by swallows the previous year, such as dead nestlings and droppings, so any parasites in these boxes presumably would have had access to hosts previously, and could have increased in number. *CI boxes* were cleaned in the same manner as C and S boxes, then we inserted compact styrofoam and a plywood floor to fill the bottom 8 cm of each box. CI boxes simulated the smaller cavity of boxes with old nest material.

In 1991, C, S, and O boxes were matched into 79 pairs, and each pair of boxes was put on a territory. 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. Each territory-type was distributed, alternately, 30–40 m apart along dikes of the marsh, and boxes within a territory were 3 m apart. This design provided a choice of two boxes to each pair of swallows. Territory occupancy was 100%.

In 1992, the boxes were redistributed as two types, C and O, arranged singly and alternately, 30–40 m apart along dikes of the marsh. In total, there were 125 boxes in the marsh, of which 112 (90%) were occupied early in the breeding season. Fifteen randomly chosen C boxes were designated as CI boxes to examine further how cavity size influenced nest building by females (Rendell and Verbeek, in press). The depth of the inserts in CI boxes approximated the mean depth of old nest material in O boxes in 1992 (mean ± SE = 7.4 ± 0.3 cm, $n = 58$).

CAPTURE AND BANDING

We captured 72 nestling females in 1991, and 108 in 1992. Birds were captured by hand, in mist nets, and using box traps (Stutchbury and Robertson 1986). Captured females received aluminum bands and were individually marked with non-toxic, acrylic paints at positions on the wing and tail. They were sexed and aged according to Hussell (1983) and Stutchbury and Robertson (1987). In 1991, females were aged as second-year (SY) and after-second-year (ASY), 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).

We banded nestlings with aluminum bands on nestling day (ND) 15. This day was chosen because: 1) young have attained peak structural size, and they are close to peak mass (i.e., ND 13; mass recession occurs after ND 13, but by ND 15, on average, only 0.3 g is lost; Zach and Mayoh

1982); and 2) the first young may fledge from a nest on ND 16 (pers. obs.). 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 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: mass/(manus)^3 (cf. Slagsvold and Lifjeld 1988).

REPRODUCTIVE SUCCESS

The characteristics of females, their reproductive output, and their choice of nest-sites may all be correlated. Consequently, to control for possible covariation of adult phenotype and reproductive success with the type of box used by a female, we switched nests after they were built. This was done within pairs of boxes at randomly chosen territories in 1991. In 1992, the switches were made between O boxes and their nearest C neighbors. CI boxes were not disturbed. As an example from 1992: if a female settled at box C5, we inserted the O5 nest material underneath the new C5 nest material. The C5 box was now considered an O box. Box O5 became a C box because we removed the old material from under the new nest, cleaned the box, and put the new material back. Nest switches were made late in the nest building stage, just prior to egg-laying. Females often built only small nests (i.e., <5 g mass) in boxes with existing nest material in both years (Rendell and Verbeek, in press), so nests were switched only at those boxes where we were sure that nest handling and manipulation would not destroy the new nest. Nests were switched at 44 of 79 (56%) territories in 1991, and at 14 of 64 (22%) neighboring C–O pairs in 1992.

We monitored breeding phenology and reproductive success during regular nest checks for 73 nests in 1991 and 105 nests in 1992. Variables recorded include: first egg, hatch, and fledging dates; duration of incubation and nestling periods; number of eggs, hatchlings, fledglings, and dead young; and the percentages of hatchlings/eggs laid, fledglings/hatchings, and fledglings/eggs laid. Nest checks were conducted every day during egg-laying, hatching, and fledging at each nest, but only every three days during the incubation and nestling periods. First hatching day equals ND 1. First fledging day is the date when the first nestling left the nest. Incubation period is the number of days from when the last egg was laid to first hatch; nestling period (to first fledge) is the number of days between ND 1 and the day the first nestling fledged; and nestling period (total) is the number of days between ND 1 and the day the last nestling fledged or died.

The outcomes of nesting attempts were divided into four groups: nests where all the young fledged, those where some young fledged, those where the entire brood died, and other. The last group includes: nests where one or both members of a pair were evicted from the nest; nests where predation occurred; and those attempts where a pair abandoned the nest for unknown reasons.

ECTOPARASITE COUNTS

We collected and counted the fowl mites, bird fleas, and blowflies in nests and boxes using several methods (Rendell and Verbeek, unpubl). We used "hand counts" (Møller 1990) for fowl mites, and for fleas and blowflies we dried nests using modified Berlese funnels (Murphy 1962), and we sifted through nests by hand after the young had fledged or died. The methods used are described in greater detail in Rendell and Verbeek (unpubl.).

STATISTICAL ANALYSIS

To control for seasonal effects on reproductive success (Stutchbury and Robertson 1988), we included only those nests where the first egg was laid before 1 June. Re-nesting attempts by females whose first attempt had failed were not included in any analyses. We combined the data for all female age classes because there were no significant differences in reproductive output or nestling size between them within boxes and years, and because female age class distributions did not differ between boxes (Rendell and Verbeek, in press). Nestling size was compared between boxes within brood sizes, using within-nest means of the mass and manus length of nestlings on ND 15. We used nonparametric statistics (SAS 1985, Siegel and Castellan 1988), and a significance level $\alpha = 0.05$. After correlation analyses, we applied sequential Bonferroni tests (Rice 1989) to determine table-wide significance levels and minimize the likelihood of committing a type-I error. Sample sizes sometimes vary between tests due to missing values.

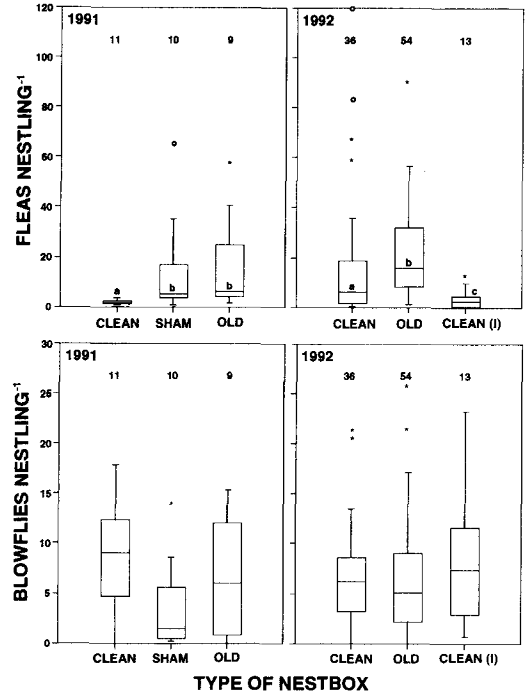

FIGURE 1. Boxplots of fleas and blowflies per nestling at different box-types in 1991 and 1992. Each boxplot shows the median, hinges (interquartile range), and the whiskers (values that are 1.5× the interquartile range from each hinge); * = outside values; o = far outside values (SYSTAT 1992). Letters denote significant differences between box-types within years for the numbers of fleas per nestling (Kruskal-Wallis tests, 1991, $H = 12.3$, $P = 0.002$; 1992, $H = 21.2$, $P = 0.0001$; df = 2; Post hoc Multiple Comparison test, Siegel and Castellan 1988). No significant differences were detected in the numbers of blowflies per nestling between box-types in either year (Kruskal-Wallis tests, all $P \geq 0.09$). Sample sizes are the numbers of broods.

RESULTS

NUMBERS OF ECTOPARASITES IN NESTBOXES

We found significantly more fleas per nestling at old and sham nests compared to clean nests in 1991, and at old nests compared to clean nests, and clean nests with inserts, in 1992 (Fig. 1). Adult fleas were observed in all nests collected in 1991 and 1992 (range = 0.3–119.4 fleas per nestling, both years combined). The highest mean number of fleas per nestling in both years (i.e., 119.4) was recorded from a C box where all the young fledged. For the sake of comparison, the mean *absolute* numbers of fleas counted from nests in our study ($\bar{x}$ ± SE [n], 1991: C = 10.7 ± 1.7 [11]; O = 89.1 ± 32.5 [9]; 1992: C = 93.4 ± 26.6 [36]; O = 112.0 ± 13.4 [54]) are lower than those reported in a one-year study employing similar methodologies in Finland (Mappes et al. 1994; C = 639 ± 193.6 [7]; O = 138 ± 32.8 [19]).

The numbers of blowflies per nestling did not differ between box-types in either year (Kruskal-Wallis [K-W] tests, all $P \geq 0.09$). Blowflies were found in 28 of 30 (93.3%) nests collected in 1991, and 96 of 103 (93.2%) nests in 1992. The percentage of nests with blowflies in our study was greater than that in other studies of the same species of blowfly (72%, Rogers et al. 1991; 66%, Roby et al. 1992), and the range of absolute numbers of blowflies per nest in this study (0–128, both years combined) is similar to those in Rogers et al. (1991) and Wittmann and Beason (1992).

We found few adult fowl mites in boxes in our study. We observed them in 54% (37/68) of boxes sampled in the population in 1991, but in <1% (1/103) of boxes in 1992. In 1991, the absolute number of mites per nest ranged from 0–300, but heavy mite infestations were rare; only two of 68 (2.9%, one S, one O box) boxes sampled that year had infestations exceeding 100 mites. Neither of these two infestations coincided with the death of an entire brood; in fact, young fledged from both boxes. The numbers of fowl mites in boxes in our study are much less than those reported from nests of the European Starling (*Sturnus vulgaris*) by Clark (1991). Because fowl mites were uncommon in our study, we chose to examine only the possible effects of fleas and blowflies on the reproductive success of Tree Swallows.

TREE SWALLOW REPRODUCTIVE SUCCESS BETWEEN YEARS

The number of young fledged per pair, the percentages of fledged young/hatchlings and fledged young/eggs laid, and the mass and condition index of nestlings were all lower in 1992 than in 1991 (Table 1). This could be attributed to higher numbers of bird fleas observed in clean and old nestboxes in 1992 compared to 1991 (Fig. 1), to significant environmental differences between the two breeding seasons, or both. The demise of entire broods in 1992 coincided with two periods of extreme weather. First, the mean air temperature at CVWMA during June 1992 (i.e., the nestling period) was warmer by 5.7°C than that

TABLE 1. Nesting phenology, reproductive success, and nestling size of Tree Swallows in 1991 and 1992, for all box-types combined. Values are means ± SE (*n* pairs).

Variable	Year	
	1991	1992
First egg date	8 May ± 0.6 (73)	7 May ± 0.6 (105)
First hatching date*	7 June ± 0.6 (66)	4 June ± 0.5 (103)
First fledging date	26 June ± 0.6 (60)	24 June ± 0.6 (87)
Incubation period (d)	14.2 ± 0.1 (66)	14.2 ± 0.2 (103)
Nestling period (d)*	20.0 ± 0.2 (60)	20.7 ± 0.2 (87)
Clutch size*	5.9 ± 0.1 (73)	5.6 ± 0.1 (105)
No. hatchlings	5.4 ± 0.1 (65)	5.3 ± 0.1 (103)
No. fledglings**	4.9 ± 0.2 (63)	3.4 ± 0.2 (103)
No. dead young**	0.6 ± 0.2 (63)	1.9 ± 0.2 (103)
% Hatchlings/eggs	92.3 ± 1.6 (65)	93.7 ± 1.2 (103)
% Fledglings/hatchlings**	91.3 ± 3.0 (63)	67.1 ± 3.8 (103)
% Fledglings/eggs**	84.3 ± 3.2 (63)	62.3 ± 3.6 (103)
Nestling mass (g)**	22.1 ± 0.2 (62)	20.4 ± 0.2 (85)
Nestling manus (mm)	24.8 ± 0.1 (62)	24.9 ± 0.1 (85)
Nestling condition index† ($\times 10^{-4}$)**	14.8 ± 0.2 (62)	13.6 ± 0.2 (85)

* $P < 0.05$, ** $P < 0.0001$, Mann-Whitney test of medians, two-tailed.
† Condition index = Mass/(Manus)^3. See METHODS for more details.

in June 1991. In 1992, 10 of the 16 (62%) instances where whole broods died occurred during 19–27 June, a period of nine consecutive days when the maximum air temperature exceeded 30°C. During nest checks, nestlings were found panting, a clear sign of heat stress. The remaining instances of whole brood death that year occurred during a severe rain storm and cold snap on 13 June when the average temperature for the day (based on 24 hourly readings) dropped from 21.5°C on 12 June, to 10°C on 13 June. Also, it is possible that weather, parasites, or both, may have contributed to the significantly longer nestling period observed in 1992. Unfortunately, we cannot distinguish conclusively which of the effects of weather and ectoparasites were most influential on nestling survivorship.

TREE SWALLOW REPRODUCTIVE SUCCESS WITHIN YEARS

In 1992, first egg and first hatching dates were significantly different between C, CI, and O boxes (Table 2). First egg and hatching dates were earlier for pairs using C boxes than for those using CI and O boxes, but neither variable was significantly different between pairs using the last two box-types. Otherwise, nesting phenology was not different for pairs using different box-types in either year (Table 2, K-W tests, all $P \geq 0.06$).

Reproductive output was not different between pairs using different boxes in either year (Table 3, K-W tests, all $P \geq 0.19$). Also, the distributions of outcomes of breeding attempts were not different between box-types in either year (Table 4). Average clutch sizes tended to be larger in clean boxes; there was a weak, but significant, positive association between cavity size (after nest switches) and clutch size, in both years, when all boxes were combined (Fig. 2).

We compared nestling size between box-types on ND 15 within broods of four, five, and six young in 1991 and 1992. Small sample sizes precluded meaningful tests with other brood sizes within years. Mass, manus, and the condition index for nestlings were not significantly different between the three box-types in either year (Table 5, K-W and M-W tests, all $P \geq 0.13$).

DID ECTOPARASITES AFFECT TREE SWALLOW REPRODUCTIVE SUCCESS?

We performed correlations between the numbers of fleas and blowflies per nestling and all measures of reproductive phenology, output and nestling size, for all nests combined in each year. Except for one test, there were no significant associations between the numbers of either of the parasites per nestling in a nest, and any measure of nesting phenology or reproductive success, after applying sequential Bonferroni table-wide corrections (all $P \geq 0.004$: 1991, $n = 29$–30 nests; 1992, $n = 80$–103 nests; *n*s vary depending on the reproductive variable). In 1991, we found a significant negative correlation between the number of fleas per nestling and clutch size

TABLE 2. Nesting phenology for pairs of Tree Swallows using different box-types in 1991 and 1992. Values are means ± SE (*n*, range).

	1991			1992		
	Clean	Sham	Old	Clean	Clean(I)	Old
First egg date*	20 May ± 0.7 (27, 132–146)	19 May ± 0.8 (23, 130–149)	16 May ± 1.5 (23, 123–151)	15 May ± 1.0^a (37, 123–145)	20 May ± 1.2^b (13, 130–145)	18 May ± 0.7^b (55, 126–151)
First hatch**	7 June ± 0.7 (24, 153–164)	7 June ± 0.9 (21, 150–168)	4 June ± 1.4 (21, 144–170)	2 June ± 1.0^a (36, 141–163)	6 June ± 1.0^b (13, 150–162)	4 June ± 0.7^b (54, 145–169)
First fledge	26 June ± 0.7 (22, 172–183)	26 June ± 0.9 (19, 171–188)	25 June ± 1.5 (19, 163–190)	22 June ± 1.2 (30, 160–184)	27 June ± 1.1 (12, 169–182)	25 June ± 0.8 (45, 162–186)
Incubation period	14.1 ± 0.3 (24, 13–18)	14.2 ± 0.2 (21, 13–18)	14.4 ± 0.3 (21, 13–17)	14.3 ± 0.3 (36, 13–25)	13.6 ± 0.2 (13, 13–15)	14.2 ± 0.2 (54, 13–20)
Nestling period–to 1st fledging	18.9 ± 0.3 (22, 16–23)	18.6 ± 0.3 (19, 16–21)	19.7 ± 0.2 (19, 18–22)	19.5 ± 0.2 (30, 17–21)	19.8 ± 0.3 (12, 18–21)	19.4 ± 0.2 (45, 17–22)
Nestling period–total	20.4 ± 0.4 (22, 18–25)	19.6 ± 0.2 (19, 18–21)	19.8 ± 0.2 (19, 18–21)	20.8 ± 0.3 (30, 18–23)	20.8 ± 0.4 (12, 18–23)	20.6 ± 0.2 (45, 18–24)

All periods in days. Range for phenology variables in Julian days: 1 June = Julian days 152 (1991), and 153 (1992).
Kruskal-Wallis tests, two-tailed, df = 2; * 1992 only, $H = 10.7$, $P = 0.005$; ** 1992 only, $H = 8.0$, $P = 0.02$. Letters indicate which groups are different, $P < 0.05$, Multiple comparison test (Siegel and Castellan 1988).

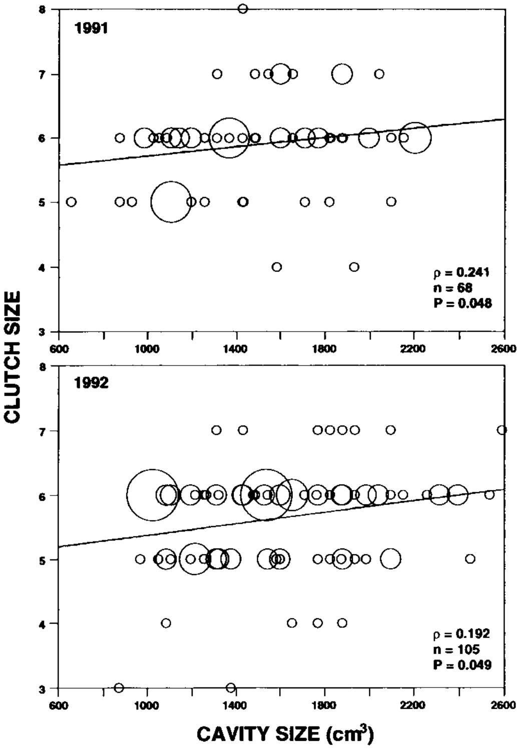

FIGURE 2. Correlation between clutch size of Tree Swallows and cavity size, for all nests combined, in 1991 and 1992. Larger circles indicate that two or more values are tied at an X-Y intercept. ρ = Spearman's rank order correlation coefficient (r_s).

(Spearman rank order correlation, $r_s = -0.53$, $n = 30$ nests, $P = 0.002$). However, this correlation was not observed in 1992 ($r_s = -0.02$, $n = 103$ nests, $P = 0.82$), and partial correlation of the number of fleas per nestling with clutch size in 1991, when controlling for cavity size (cf. Fig. 2), was not significant ($r_s = -0.34$, $P = 0.07$).

We compared the numbers of parasites in nests where some or all of the young fledged with those in which the entire brood died in 1992. The numbers of fleas and blowflies per nestling were not different between nests where young fledged and those where a whole brood died (mean ± SE (*n*); fleas per nestling, fledged young = 18.6 ± 2.4 (87), whole brood died = 12.8 ± 3.2 (16); blowflies per nestling, fledged young = 6.9 ± 0.6 (87), whole brood died = 5.4 ± 1.4 (16); Mann-Whitney [M-W] tests, all $P \geq 0.15$). Instances where an entire brood died were rare in 1991, so this comparison was only possible using 1992 data.

TABLE 3. Reproductive output for pairs of Tree Swallows using different box-types in 1991 and 1992. Values are means ± SE (*n*, range). No significant differences were detected for any measure in either year (Kruskal-Wallis tests, all $P \geq 0.19$).

	1991			1992		
	Clean	Sham	Old	Clean	Clean(I)	Old
Clutch size	6.0 ± 0.2 (27, 4–7)	6.0 ± 0.1 (23, 5–7)	5.8 ± 0.2 (23, 5–8)	5.8 ± 0.1 (37, 4–7)	5.5 ± 0.2 (13, 5–7)	5.5 ± 0.1 (55, 3–7)
# Hatchlings	5.6 ± 0.2 (24, 3–7)	5.5 ± 0.2 (21, 4–7)	5.1 ± 0.3 (20, 3–7)	5.3 ± 0.2 (36, 2–7)	5.2 ± 0.2 (13, 4–7)	5.3 ± 0.1 (54, 2–7)
# Fledglings	4.9 ± 0.4 (24, 0–7)	5.1 ± 0.3 (20, 0–6)	4.7 ± 0.3 (19, 2–7)	3.4 ± 0.4 (36, 0–7)	4.1 ± 0.5 (13, 0–6)	3.3 ± 0.3 (54, 0–6)
# Dead Young	0.7 ± 0.4 (24, 0–7)	0.4 ± 0.3 (20, 0–6)	0.6 ± 0.4 (19, 0–6)	1.9 ± 0.4 (36, 0–7)	1.2 ± 0.5 (13, 0–6)	2.0 ± 0.3 (54, 0–6)
% Hatch/clutch	94.2 ± 2.0 (24, 71–100)	92.6 ± 2.2 (21, 67–100)	89.7 ± 4.3 (20, 43–100)	92.1 ± 2.4 (36, 33–100)	94.6 ± 2.4 (13, 80–100)	94.4 ± 1.5 (54, 50–100)
% Fledge/hatch	88.4 ± 5.9 (24, 0–100)	92.6 ± 5.2 (20, 0–100)	93.7 ± 3.9 (19, 33–100)	66.9 ± 6.5 (36, 0–100)	78.1 ± 9.4 (13, 0–100)	64.6 ± 5.4 (54, 0–100)
% Fledge/clutch	82.9 ± 5.8 (24, 0–100)	86.6 ± 5.2 (20, 0–100)	83.7 ± 5.6 (19, 33–100)	60.6 ± 6.0 (36, 0–100)	73.8 ± 9.2 (13, 0–100)	60.6 ± 5.1 (54, 0–100)

DISCUSSION

We found little evidence that the presence of old material in a box affects the reproductive success of Tree Swallows, at least within the range of parasite loads and cavity sizes seen in this study, indicating that re-use of cavities is not necessarily a disadvantage to this species. Swallows using boxes with and without old nest material did not differ significantly in reproductive output, despite the fact that birds in boxes with old nests experienced higher loads of fleas (Fig. 1), and that birds using clean boxes often had the added advantage of using a larger cavity (Fig. 2; see also Rendell and Robertson 1993). We found no significant associations between the numbers of parasites per nestling and any reproductive variables. Also, the numbers of parasites per nestling at boxes where the young fledged, as compared with those where entire broods died, did not indicate that parasites were more numerous at failed nests. This suggests that neither the combined totals of the three types of parasites in this study, nor each species individually, had a significant detrimental effect on the reproductive success of Tree Swallows. Our results would be expected if the numbers of parasites were relatively low compared to other studies. However, the number of fleas per nestling in our study greatly exceeded that observed in a recent study of Great Tits (*Parus major,* Richner et al. 1993), and in that study fleas appeared to have a strong negative impact on reproductive output. Also, Mappes et al. (1994) reported flea loads in nests of Pied Flycatchers (*Ficedula hypoleuca*) that were *higher* than those in our study, and yet found no effect on reproductive success.

TABLE 4. Outcomes of nesting attempts for pairs of Tree Swallows using different box-types in 1991 and 1992. Values are percentages of the sample size for each box-type. See METHODS for an explanation of the outcome groups.

	1991			1992		
Outcome	Clean ($n = 28$)	Sham ($n = 25$)	Old ($n = 26$)	Clean ($n = 41$)	Clean(I) ($n = 14$)	Old ($n = 57$)
All young fledged	46.4	44.0	42.3	26.8	35.7	38.6
Some young fledged	35.7	32.0	34.6	46.3	50.0	40.4
All young died	7.1	4.0	0.0	14.6	7.1	15.8
Other	10.7	20.0	23.1	12.2	7.1	5.3

Distributions are not significantly different between box-types within years, Chi Square test, 1991: $\chi^2 = 3.19$, $P = 0.78$; 1992: $\chi^2 = 3.36$, $P = 0.76$; df = 6 both years.

TABLE 5. Nestling mass (g), manus (mm), and condition index $(\times 10^{-4})$† on day 15 from broods of four to six young, in different box-types, during 1991 and 1992. Values are means ± SE (*n* broods). No significant differences were detected between box-types in either year (Kruskal-Wallis and Mann-Whitney tests, all $P \geq 0.13$).

		1991			1992		
Brood size		Clean	Sham	Old	Clean	Clean(I)	Old
Four	Mass	23.4 ± 0.6 (3)	—	21.0 ± 1.6 (3)	21.1 ± 0.4 (8)	—	21.2 ± 0.6 (7)
	Manus	26.0 ± 1.6 (3)	—	24.9 ± 1.1 (3)	25.5 ± 0.4 (8)	—	25.2 ± 0.4 (7)
	Index	14.0 ± 2.3 (3)	—	13.9 ± 1.2 (3)	13.3 ± 0.7 (8)	—	13.5 ± 0.9 (7)
Five	Mass	22.5 ± 0.8 (6)	22.4 ± 0.2 (8)	22.9 ± 0.2 (7)	21.4 ± 0.7 (7)	20.2 ± 0.6 (8)	20.6 ± 0.4 (20)
	Manus	24.6 ± 0.5 (6)	25.0 ± 0.2 (8)	24.7 ± 0.5 (7)	24.6 ± 0.3 (7)	25.1 ± 0.2 (8)	25.2 ± 0.2 (20)
	Index	15.6 ± 0.6 (6)	14.6 ± 0.4 (8)	15.8 ± 1.0 (7)	14.7 ± 0.9 (7)	12.8 ± 0.6 (8)	13.1 ± 0.5 (20)
Six	Mass	21.4 ± 0.6 (9)	21.8 ± 0.4 (10)	21.6 ± 0.5 (4)	19.6 ± 0.5 (12)	—	20.3 ± 0.3 (11)
	Manus	24.7 ± 0.2 (9)	24.7 ± 0.3 (10)	24.6 ± 0.3 (4)	24.7 ± 0.3 (12)	—	24.4 ± 0.2 (11)
	Index	14.5 ± 0.5 (9)	14.9 ± 0.4 (10)	14.6 ± 0.4 (4)	14.1 ± 1.0 (12)	—	14.4 ± 0.5 (11)

† Index = Mass/$(\text{Manus})^3$. See METHODS for more details. — = Insufficient broods for analysis.

We caution that our measurements of reproductive output are rough measures of success, and they do not necessarily indicate the likelihood of recruitment of offspring to the breeding population in subsequent years. Parasitized nestlings in other studies were morphometrically similar to relatively unparasitized young, but some studies showed that parasitized nestlings suffered from anemia (Richner et al. 1993), which may have serious consequences for immediate post-fledging survival. Also, relative to unparasitized young, parasitized young may be more likely to contract viral protist and bacterial infections from ectoparasites (e.g., Warren 1994), again with unknown consequences for their survival after fledging.

Swallows using boxes with old material in 1992 began nesting later than conspecifics in clean boxes. Oppliger et al. (1994) reported delayed laying by Great Tits in boxes inocculated with fleas, so Tree Swallows may have been avoiding boxes with old nest material and the higher ectoparasite loads within. However, that same year they delayed nesting in clean boxes with inserts as well, suggesting that, as in the nestbox preference experiments in Rendell and Verbeek (in press) and Rendell and Robertson (1993), they may simply have been avoiding settling at nestboxes with smaller cavities. Unfortunately, we do not have data on settling dates at CVWMA.

There was an association between higher numbers of bird fleas in clean and old nestboxes in 1992 compared to 1991, and reduced reproductive success and nestling size in the former year. We do not know whether this was because of parasites, weather, or both. Mason (1944) stated that the detrimental effects of blood loss to parasites may only arise during periods of high energy requirements and reduced food supply. In support of this, de Lope et al. (1993) reported that, late in their breeding season, when conditions for nesting are apparently worse relative to earlier months, House Martins (*Delichon urbica*) with nests infested with the House Martin Bug (*Oeciacus hirundinis*) had considerably lower reproductive success compared to other late nesters whose nests were parasite-free, and compared to early nesters with infested nests. In our study, it is possible that local insect availability was reduced during the extreme hot and cold spells in the Creston Valley in June 1992, and this, combined with the high numbers of fleas, may have caused the observed brood loss.

Møller (1989) noted that researchers typically remove old nest material from boxes after each breeding season, and he hypothesized that this introduces an experimental artifact to box studies that calls the validity of results from all such studies into question. He concluded that researchers should interpret the results of these studies with caution, and that generalizations should not be applied from studies of birds breeding in boxes to those using natural tree holes, or even other species, until ecologists have a better appreciation of the possible costs to hole-nesters associated with breeding in cavities where parasites are numerous.

This critique has stimulated much recent research, and the criticisms are partly justified. However, after the completion of several studies on this topic, it now appears that Møller's concerns are not justified in every population. Parasites may be more numerous in cavities with old material (Fig. 1), although this may apply only to particular kinds of parasites (e.g., bird fleas). Many factors contribute to the presence and numbers of parasites in nests, including the life-cycle of each species (Rendell and Verbeek, unpubl.), so the accumulation of old material in a cavity does not necessarily mean that parasites will be common as well. The presence of old material in cavities can affect cavity selection and nest building in hole-nesters (e.g., Tree Swallows, Rendell and Verbeek, in press), although not all species (e.g., Eastern Bluebirds, *Sialia sialis,* Davis et al. 1994; House Wrens, Thompson and Neill 1991, Johnson 1996; Pied Flycatchers, Mappes et al. 1994), perhaps due to differences between species in their natural history. In fact, Eastern Bluebirds and Pied Flycatchers apparently prefer nests with old material. Further, some studies of cavity-nesting birds have found that a variety of parasites affect their breeding phenology (Oppliger et al. 1994) and reproductive success (Moss and Camin 1970, Pinkowski 1977, Capreol 1983, Clark and Mason 1988, Fauth et al. 1991, de Lope et al. 1993, Winkler 1993, Richner et al. 1993, Eeva et al. 1994, Møller et al. 1994), while as many studies have not (Gold and Dahlsten 1983, Demas 1989, Eastman et al. 1989, Johnson et al. 1991, Roby et al. 1992, Wittmann and Beason 1992, Johnson and Albrecht 1993, Mappes et al. 1994, this study; see also studies in Loye and Zuk 1991).

Møller (1989) hypothesized that birds re-using old nests would experience reduced reproductive success. To date, the evidence in support of this hypothesis is equivocal; reproductive success is not necessarily lower for birds re-using old nests, nor for birds inhabiting nests that were experimentally inocculated with parasites. To date, the combined results from studies of the effects of parasites and old nest material on the breeding ecology of hole-nesting birds suggest there is little opportunity for generalization from one study to another (Koenig et al. 1992).

In conclusion, we recommend two avenues for future research. First, simultaneous long-term studies of hole-nesting birds, local climate, and the ectoparasites in boxes would contribute greatly to our understanding of the interactions between ectoparasites and their hosts. Many interesting questions remain unanswered concerning what factors contribute to fluctuations in parasite populations in cavities. For example, once the population of an ectoparasite rises in a nest, does it stabilize for several host breeding seasons, or exhibit cyclic fluctuations in magnitude, possibly in response to predators, parasitoids, or environmental change? Also, if cavity-nesting birds can recognize nests infested with parasites (e.g., Barclay 1988; Rendell and Verbeek, in press), are some cavities avoided for one or more seasons until parasite numbers decline for lack of a host? To date, research in this field has typically considered only a "snap-shot" in time and space of the relationship between parasite and host. Second, to complement such studies, researchers could develop qualitative and quantitative models of lifetime reproductive success which include parameters estimating the frequency and severity of ectoparasitism in cavities of these species. By manipulating realistic parameters such as brood size of host and magnitude of cyclic fluctuations in parasite numbers in cavities using computer programs, ecologists could simulate the dynamics of host-parasite interactions in cavities within and between breeding attempts throughout the lifetimes of individuals. This latter approach may be the most practical way for ecologists to further examine the potential effects of ectoparasitism on the breeding ecology of hole-nesting birds.

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