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REMOVAL OF OLD NEST MATERIAL FROM THE NESTING SITES OF HOUSE WRENS: EFFECTS ON NEST SITE ATTRACTIVENESS AND ECTOPARASITE LOADS

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Abstract.—This study tested whether removal of old nests from nest boxes affects the attractiveness of boxes to House Wrens (*Troglodytes aedon*) in a Wyoming, USA, population. Over 2 yr, 59 pairs of wrens were given a choice between two boxes mounted <2 m apart. One box contained an old wren nest, the other box was empty. Wrens showed no preference for either type of nest box; 32 (54%) and 27 (46%) pairs used boxes with and without old nests, respectively. Wrens did, however, avoid re-using old nests if these nests were heavily soiled. Pairs that chose boxes with and without old nests spent equal amounts of time in nest preparation and did not differ significantly in reproductive output. Young raised in boxes that had contained old nests did not experience higher loads of ectoparasitic blow fly (*P. parorum*) larvae, probably because blow flies, unlike other types of nestling ectoparasites, do not overwinter in nests.

REMOCIÓN DE MATERIALES DE NIDO VIEJOS DE LAS ÁREAS DE ANIDAJE DE *TROGLODYTES AEDON*: EFECTOS EN LA ATRACTIVIDAD DE ÁREAS DE ANIDAJE Y EN LAS CARGAS DE ECTOPARÁSITOS

Sinopsis.—Este estudio probó si la remoción de nidos viejos de ias cajas de nido afecta la atractividad de esas cajas a *Troglodytes aedon* en una población de Wyoming, USA. A través de 2 años se le ofreció la oportunidad de anidar en una de dos cajas montadas <2 m aparte a 59 parejas de *Troglodytes aedon.* Una caja contenía un nido viejo de *Troglodytes aedon,* la otra estaba vacía. Las parejas no mostraron preferencia por ningún tipo de nido; 32 (54%) y 27 (46%) parejas usaron cajas con y sin nidos respectivamente. Sin embargo, las aves evitaron usar nidos viejos si estos estaban muy sucios. Parejas que seleccionaron cajas con y sin nidos viejos invirtieron cantidades iguales de tiempo en preparar el nido y no difirieron significativamente en el esfuerzo reproductivo. Juveniles criados en cajas conteniendo nidos viejos no experimentaron cargas mayores de larvas de moscas parasiticas (*P. parorum*), probablemente debido a que estas moscas no pasan los inviernos en los nidos a diferencia de otros tipos de ectoparásitos de pichones.

Nests built in sites protected from wind and moisture often remain intact from one breeding period to another thereby allowing their re-use. Re-use of an old nest can potentially save birds both time and energy which could enhance reproductive output (Conrad and Robertson 1993, Gauthier and Thomas 1993, Shields et al. 1988). Also, if birds can distinguish between sites that were and were not used successfully in the previous breeding period, judging perhaps by the the amount of fecal material in the nest, then they may enhance their own chances for success by avoiding unsuccessful sites.

Nest re-use also has potential disadvantages. Nests and the structures that support them (e.g., snags, cliff faces), can lose structural integrity over time making old nests more prone to falling. Recent studies suggest that some nest predators remember and re-visit nest sites plundered in previous breeding periods (e.g., Nilsson et al. 1991, Sonerud 1993). If birds cannot identify plundered nests, then birds re-using nests may face increased risk of nest predation. Birds may also face competition for a previously used site if its former owners appear with intentions also to use the site. Such competition can result in nest destruction or at least delayed breeding (L. S. Johnson, unpubl. data; Jakobsson 1988; Walton and Nolan 1986).

A fourth potential disadvantage to nest re-use and one that has received substantial attention recently is increased exposure to nest-dwelling ectoparasites. Some ectoparasites (e.g., cimicids, fleas and mites) remain in old nests between breeding periods presumably to infest the next birds using the nests (e.g., Barclay 1988, Loye and Zuk 1991, Oppliger et al. 1994). Møller (1989) argued that results of certain nest box studies are potentially biased, in part because researchers usually remove old nesting material from boxes between breeding seasons. Removal of old nesting material could reduce ectoparasite loads for birds subsequently using boxes which, in turn, may increase nest site attractiveness and reproductive success. At the time that Møller raised his concerns, no published information existed on how removal of nest material from boxes affected subsequent box use, ectoparasite numbers, or reproductive success. Clearly information of this sort is necessary to evaluate fully Møller's concerns.

Here I report on the effects of removing old nests from boxes used by a Wyoming population of the House Wren (*Troglodytes aedon*). My first objective was to determine whether removal of old nest material from a box affected its attractiveness as a nest site, as reflected by its probability of subsequent use by wrens. I also asked whether broods raised in boxes with old nests would incur greater loads of ectoparasites than birds raised in boxes that were emptied between seasons. Nestling wrens in the study population are parasitized primarily by haematophagous larvae of the blow fly *Protocalliphora parorum* (Diptera: Calliphoridae; Johnson and Albrecht 1993). Blow fly larvae parasitize nestlings in a variety of cavity-nesting species throughout the northern holarctic (Iwasa and Hori 1990, Owen 1954, Rognes 1984, Sabrosky et al. 1989). Unlike many other nest-dwelling ectoparasites, however, blow flies do not overwinter in nest cavities. It therefore seemed unlikely that numbers of blow flies in boxes with and without old nests would differ.

METHODS

I conducted this study during the 1993 and 1994 breeding seasons on several cattle ranches near Big Horn, Wyoming, USA. Wrens on these ranches occupy patchily distributed bands of woodlands growing along creeks and rivers that flow through pastures and hayfields.

Nest site preference experiment.—Approximately 100 nearly identical nest boxes (internal dimensions: $10.0 \times 9.5 \times 18.5$ cm) were present in the study area during the 1992 breeding season, the year before this study began. During the 1992 season, I monitored the success of wrens using all boxes and identified boxes from which relatively large broods fledged ($\geq$4 young fledged from clutches of 5–8 eggs). At the end of the season, I left old nests in 40 of these boxes and removed old nests from the remaining boxes. Following Thompson and Neill (1991), I refer to boxes with intact old nests as "dirty" boxes, and boxes from which I removed old nests as "clean" boxes. With the exception of five dirty boxes left attached to trees, I stored all boxes in an unheated shack over the subsequent winter. It is important to note that at the time boxes were collected for storage, all blow fly larvae reared in boxes would have pupated, eclosed, and dispersed from boxes (see discussion of parasite's life history below). All boxes were checked visually for adult flies before collection and none were seen.

Before wrens arrived from migration in 1993, I erected one clean and one dirty box side-by-side at 40 different locations on one half of my study site, making certain that neither of the two boxes erected at one location were present at the same location in the previous year. At each location, I mounted the two boxes 0.6–2.2 m apart ($\bar{x}$ = 1.0 m) on identical, greased metal poles, randomly assigning boxes to the two poles on which they were mounted. At all locations, I took care to erect both boxes at the same height, facing the same direction, and at equal distances from similar cover. This often required trimming branches near boxes and rearranging brush below boxes.

In this same year, 1993, nest boxes were present in other parts of my study area for use in other studies. During the course of the season, I noted which of these boxes produced ≥4 fledglings. At the end of the season, I left nests in all such boxes (approximately 50) and removed old nests from the remaining boxes. I left all boxes, clean and dirty, attached to trees or metal poles during the subsequent winter.

Before wrens arrived in 1994, I collected all boxes and then erected clean and dirty boxes in pairs as described above (0.6–2.6 m apart, $\bar{x}$ = 1.1 m) on parts of my study area not used for this experiment in 1993. Male and female House Wrens tend to return to or near locations that they occupied in the previous year, so my use of different parts of the study area in 1993 and 1994 helped ensure that I had little (if any) overlap in the two sets of birds observed in the two years. Approximately 50% of birds involved in 1993 trials were marked. None of the marked birds were involved in the 1994 trials.

At least every other day in both years of the study, I noted in detail the contents of clean and dirty boxes at each location and the behavior of any wrens present. In House Wrens, the male establishes a territory with a potential nest cavity before attracting a mate. If that cavity contains an old nest, the male may remove the old grass and feather nest lining leaving a well-formed cup of >400 small sticks. If the cavity does not contain an old nest, the male will add sticks to construct a partial cup. Males "show" potential nest cavities to females when females visit their territories. Females then complete nest construction with little or no help from males. I assumed that a female had chosen a particular nest box when I observed her making repeated trips with nest material into one box (females never started building in both clean and dirty boxes simultaneously). At this point, I removed the other, rejected nest box from the territory. I then monitored the breeding progress of wrens in their chosen box. I counted and weighed nestlings 11 d after hatching began when nestlings are at or near their peak mass. After young fledged I removed nests from boxes to determine numbers of blow fly larvae in nests.

In both years of study, some trials failed for a variety of reasons. For example, in some cases males claimed pairs of boxes, modified nests in one or both boxes, and then disappeared before mating. Observations on these pairs of boxes were terminated. In other cases, I found wrens using one box and wasps or bees in the other box. As I did not know whether wrens chose their box before wasps or bees arrived, I omitted these cases from analyses.

In total, there were 59 instances over the 2 yr of study where wrens had a clear choice of a clean and dirty box situated side-by-side. This sample size provides adequate statistical power (i.e., ≥80%, Cohen 1988) to detect a real departure from a random choice of boxes of about 16% or more (i.e., ≥66% of wren pairs prefer one type of box over the other). As the two boxes available to each pair differed essentially only in the presence or absence of an old nest, a departure of 16% or more from random choice seemed to be a reasonable expectation if a marked preference for one or the other types of boxes existed.

Ectoparasites and determination of their numbers.—Larval *P. parorum* feed primarily on the nestlings of small, cavity-nesting birds (Sabrosky et al. 1989). Adult female flies lay eggs in host nests only after host eggs have hatched (Gold and Dahlsten 1989). Larvae live in nest material and feed intermittently on the blood of nestlings. Third instar larvae may attain masses >100 mg before host young fledge. After hosts fledge, larvae pupate in nests and emerge from cavities within 2–5 wk. *P. parorum* is univoltine and both sexes overwinter as adults (Gold and Dahlsten 1989), possibly under the bark of trees (Sabrosky et al. 1989).

After a brood fledged, I removed its nest from the nest box and carefully sorted through nest material removing any blow fly larvae or pupae. The actual number of blow flies present in a nest is a poor measure of the intensity of parasitism because the size of larvae at time of host fledging varies substantially between nests, and large larvae will have consumed more host blood than small larvae. I therefore calculated a number of "larval equivalents" present in a nest by dividing the total mass of larvae in the nest by 0.07, the mean mass (g) of individual larva in 56 nests examined in a previous study (Johnson and Albrecht 1993). In addition, I assumed that each pupated individual had attained a mass of 0.12 g as a larva, which was the mean mass of the two largest larvae in eight nests observed previously. Thus total "larval equivalents" for a nest equaled the (mass of larvae/0.07) + (number of pupae × 0.12)/0.07.

I report all means ± 1 SE and all statistical tests are two-tailed. To minimize the number of statistical tests made, I combined data for the two years of study in a single analysis that controlled for effects of year, although this was not often possible due to departures from normality.

TABLE 1. Numbers of House Wren pairs choosing to use either a nest box containing an old wren nest or an empty nest box, when given a choice between the two.

Year	Number of pairs using the box	
	With old nest	Without old nest
1993	18 (58%)	13 (42%)
1994	9 (32%)	19 (68%)

Log-linear test (William's correction): $G_1 = 3.94$, $P < 0.05$.

RESULTS

Over the two years of study, wrens did not show a preference for either clean or dirty nest boxes: 27 (46%) and 32 (54%) of the 59 pairs observed used clean and dirty boxes, respectively (binomial test: $P > 0.60$). The wrens' use of the two types of boxes differed significantly between years; most wren pairs chose clean boxes in 1993 but dirty boxes in 1994 (Table 1).

Dirty boxes differed substantially in the degree to which the nest within was soiled during previous use and this influenced subsequent use of the box. Before wren settlement began, I classified dirty boxes as "heavily soiled" if nests within were covered with a thick cake of dried feces, and "lightly soiled" if nests contained very little fecal material (other boxes were considered moderately soiled). Wrens clearly avoided heavily soiled, and preferred lightly soiled, dirty boxes (Table 2). To determine whether some heavily soiled boxes might be completely unusable, in both years I took all heavily soiled boxes that wrens left untouched and remounted them in areas that were currently unoccupied by wrens. A male claimed each of these boxes and all males attracted a mate except for one male that established himself very late in the season. All females attracted completed nests and laid normal-sized clutches of eggs.

On 52 of the 59 territories where wrens chose between a clean and dirty box, males occupied the territory at least one full day before attracting a female and I was able to record male response to boxes in the absence of a female. Most males showed a preference for either the clean or dirty box prior to female arrival as evidenced by their nest-preparation

TABLE 2. Relationship between a preference for nest boxes with old nests over boxes without old nests and the degree to which the old nest involved was soiled during previous use. Data combined for two years of study. Trials that involved "moderately soiled" dirty boxes were excluded from analyses.

Condition of nest in box with old nest	Number of pairs using the box	
	With old nest	Without old nest
Heavily soiled	3 (27%)	8 (73%)
Lightly soiled	15 (68%)	7 (32%)

Log-linear test (William's correction): $G_1 = 4.80$, $P < 0.03$.

TABLE 3. Degree of concurrence by male and female House Wrens in their preference for nest boxes with old nests or without old nests. Data combined for two years of study. Note: four cases in which males built in both types of nests boxes are excluded (see text).

When male chooses:	Female subsequently chooses	
	Box with old nest	Box without old nest
Box with old nest	26 (84%)	5 (16%)
Box without old nest	1 (6%)	16 (94%)

Log-linear test (William's correction): $G_1 = 29.72$, $P < 0.001$.

activity. In only four of 52 cases (8%) did males extensively prepare both boxes, removing the entire nest lining from the dirty box and building a partial stick cup in the clean box. In 31 cases (60%), males removed all or part of the old lining in the dirty box while essentially ignoring the clean box. In 17 cases (33%), males ignored the dirty box but added numerous sticks to the clean box. A male's mate usually accepted his choice; females chose the box prepared by their mate significantly more often than expected by chance (Table 3).

In 17 and 21 cases where pairs used clean and dirty boxes, respectively, I was able determine the time that elapsed from the day the female began nest-building in earnest to the day that she laid her first egg. Both females using clean boxes and those using dirty boxes began egg-laying an average of 8.0 (±0.4 SE) d after beginning nest construction (means are adjusted

TABLE 4. Measures of reproductive output and intensity of infestation with blow fly larvae for House Wrens using nest boxes with old nests and boxes without old nests. Shown are means ± 1 SE (*n*).

Measure	Year	Wren pairs using boxes		Statistic[a]	*P*
		Without old nests	With old nests		
Clutch size	1993	6.6 ± 0.3 (17)	7.1 ± 0.3 (10)[b]	$Z = 0.90$	>0.35
	1994	7.3 ± 0.3 (9)	7.2 ± 0.3 (17)	$Z = 0.90$	>0.65
No. of young fledged	1993	5.3 ± 0.6 (16)	4.1 ± 0.8 (11)	$Z = -1.11$	>0.25
	1994	5.6 ± 0.6 (9)	6.5 ± 0.3 (15)	$Z = -1.43$	>0.15
No. fledglings per egg	1993	0.82 ± 0.1 (15)	0.66 ± 0.1 (10)	$Z = -1.18$	>0.20
	1994	0.74 ± 0.1 (9)	0.91 ± 0.1 (15)	$Z = -1.63$	>0.10
Mean mass of young (g)[c]	1993	10.4 ± 0.3 (15)	9.6 ± 0.5 (9)	$t = 1.72$	>0.09
	1994	9.6 ± 0.3 (9)	10.2 ± 0.2 (15)	$t = -1.69$	>0.10
No. of larvae equivalents[d]	1993	73.5 ± 8.9 (15)	58.7 ± 9.0 (10)	$Z = -1.08$	>0.25
	1994	2.1 ± 2.1 (8)	11.7 ± 7.9 (15)	$Z = -0.72$	>0.45

[a] *Z*-scores are for Wilcoxon Rank Sum tests.

[b] One or more eggs were lost from one nest during laying so clutch size could not be determined. This also reduced sample size for "fledglings per egg".

[c] Analyses involved brood means to avoid pseudoreplication.

[d] See Methods for a description of how ectoparasite loads were calculated.

for year effects; two-way ANOVA: $F_{1,34} < 0.01$, $P > 0.99$). Thus, the presence of an old nest in a box did not reduce time to egg-laying.

Wren pairs using clean and dirty nest boxes did not differ significantly in number of eggs laid, number of young fledged, number of young fledged per egg laid, or the mean mass of young produced (Table 4). These results remain unchanged when I analyze only those nests producing at least one fledgling (data not shown for brevity).

Wren pairs using clean and dirty boxes did not experience significantly different infestations of blow fly larvae in either year of this study (Table 4). Relatively few larvae were present in 1994, however. Many adult flies apparently died in the spring of 1994 when a late snowstorm and cold snap followed several weeks of warm weather.

DISCUSSION

House Wrens in the Wyoming study population showed no preference for boxes from which old nests had been removed over boxes with old nests. The lack of preference for "clean" boxes may be due in part to the fact that using a clean box provides birds no advantage in terms of reducing loads of haematophagous blow fly larvae, the dominant ectoparasite afflicting nestlings in the study population. This finding, in turn, probably reflects the fact that blow flies do not overwinter in nests. W. Rendell and N. Verbeek (pers. comm.) also found no differences in numbers of blow fly larvae infesting Tree Swallows (*Tachycineta bicolor*) using boxes with and without old nests in British Columbia.

My study involved only first broods that were reared relatively early in the season. Wrens that raise one brood early in the season often attempt to raise a second brood. A question arises as to whether birds might avoid dirty boxes used earlier in the *same* season if flies "reared" on a first brood will attack a second brood reared in the same nest site. This should not occur in the study population because the blow fly that parasitizes wrens, *P. parorum,* is univoltine (Gold and Dahlsten 1989). It remains unclear, however, whether other species of blow flies with different hosts breed more continuously (Bennett and Whitworth 1991).

Use of a "dirty" box with an old nest did have one obvious advantage to wrens: they did not need to construct a base cup of small sticks within the box. When using an old nest, wrens removed and replaced only the soft nest cup lining, not the sticks that support the lining. Boxes contain an average of about 500 sticks which wrens add one stick at a time. Thus, not having to build a cup should save birds considerable time and energy and perhaps will lessen their risk of predation. The only instances in which wrens clearly avoided boxes with old nests were when linings of these nests were covered with a thick cake of feces which I suspect made removal of the old lining unusually difficult. That wrens strongly preferred to use boxes with old nests when these nests were lightly soiled is consistent with this argument.

In a nest box choice experiment similar to my own, Davis et al. (1994) found that Eastern Bluebirds (*Sialia sialis*) in a Kentucky population *pre-*

fer boxes with old nests over empty nest boxes. They suggested that bluebirds may be attracted to boxes with old nests because *Nasonia* wasps, which parasitize blow fly pupae, overwinter in nests. *Nasonia* wasps also attack blow fly pupae on my Wyoming study site. Birds would seem to have little to gain by associating with wasps, however, because wasps do not attack blow flies until after the period of feeding on nestlings has ended.

House Wrens that used clean and dirty boxes in my study did not differ significantly in reproductive output. Although this result is consistent with their lack of preference for one type of box, it is unclear whether under natural conditions, birds using clean and dirty nest sites would also experience similar reproductive success and it is under these conditions that nest choice strategies evolved. As noted above, for some species nests built in previously used cavities are more prone to predation. As I mounted boxes on greased poles, I eliminated any predation cost of using an old nest site.

I have implied that when birds are afflicted with ectoparasites that, unlike blow flies, do overwinter in nests, birds should be less likely to use old nests, and should breed less successfully when they do use such nests (cf. Barclay 1988, Brown and Brown 1986, Loye and Carroll 1991). Even with only a few studies of cavity-nesting birds now completed, it is already clear that this will not always be true (e.g., contrast the results of Oppliger et al. 1994 and Orell et al. 1993). The study most relevant to my own is that of C. F. Thompson and co-workers on an Illinois population of House Wrens in which nestlings are parasitized only by haematophagous mites (Dermanyssidae), not blow flies (e.g., see Thompson and Neill 1991). Although dermanyssid mites overwinter in nest boxes, Illinois wrens show a significant preference for boxes with old nests and do not experience reduced reproductive success when using old boxes (C. F. Thompson, pers. comm.).

In conclusion, this study shows that in one population of House Wrens, removal of old nests from boxes does not increase the attractiveness of boxes as nest sites. This result may reflect the fact that wrens using boxes with old nests do not incur higher loads of ectoparasitic blow fly larvae, probably because blow flies do not overwinter in old nests. I do not want to suggest, however, that removal of old nests from boxes will be inconsequential when dealing with populations that are afflicted primarily by blow flies. Continual removal of nests from boxes shortly after young fledge may eventually reduce blow fly numbers, especially when flies are relatively host-specific. This, in turn, could influence reproductive success and other factors. Unless there is some overriding benefit to emptying nest boxes (e.g., to monitor nest-building activity or to enhance recovery of a species), for most long-term behavioral and ecological studies it would seem prudent to follow what is "natural" and leave old nests in boxes at least until adult flies have emerged and dispersed.

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