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NEST BUILDING IN HOUSE WRENS

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Abstract.—Recommendations for building nest boxes for House Wrens (*Troglodytes aedon*) include slot rather than hole entrances and small rather than large cavity sizes. To determine how these parameters influenced nest-building efforts by male and female House Wrens, wrens were provided with boxes that differed in entrance type (slot vs. hole) and depth (8.9 vs. 16.5 cm from entrance to nest box floor). To collect data on nest mass during nest building, each nest box was fitted with an insert made from a half-gallon waxed-paper carton. Inserts containing nests were removed from nest boxes, weighed and replaced without disturbing nest building. At the completion of nesting, the inserts were removed and sticks in nests were weighed and counted. Nest-building costs for females, which added the cup lining, did not differ among nest types, but costs for males, which filled the cavities with sticks, were dependent on box depth. Boxes with wide, slot-shaped entrances were more likely to contain an active nest (i.e., at least one egg laid) than were hole-entrance boxes regardless of cavity depth, apparently because males could more readily carry sticks through slots than holes.

CONSTRUCCIÓN DEL NIDO EN *TROGLODYTES AEDON*

Sinopsis.—Las recomendaciones para construir cajas de anidamiento para individuos de *Troglodytes aedon* incluyen que se construyan entradas en forma de ranura (en vez de hueco) y cavidades pequeñas. Para determinar como estos parámetros influyen en el esfuerzo por parte de la pareja en la construcción del nido, se le proveyó a un grupo de aves, con cajas que diferían en el tipo de entrada (ranura vs. hueco) y profundidad de las mismas (8.9 vs. 16.5 cm desde la entrada hasta el piso de la caja). Para tomar datos sobre el peso del nido durante la fase de construcción, cada caja de anidamiento fue forrada internamente con envaces de cartón encerados con capacidad para ½ gal. Las cubiertas de cartón, dentro de las cuales se comenzaron a construir nidos, eran fácilmente removidas de la caja de madera, pesadas y luegos devueltas a la caja sin sufrir cambios o interrumpir el anidamiento. Al ser completado el nido, las cubiertas de cartón eran removidas y las pajas en estas contadas y pesadas. El costo energético de las hembras, el cual incluye el forrar el nido por dentro, no difirió entre los distintos tipos de nidos. No obstante, el costo de los machos, el cual incluye el colocar pajas en el nido, varió de acuerdo a la profundidad de la caja. Aquellas cajas con entradas anchas en forma de ranura fueron más propensas a contener nidos activos (ej. las aves pusieron al menos un huevo en éstos) que cajas con entradas en forma de hueco (no afectó la profundidad de la caja). Aparentemente, los machos pueden depositar más fácilmente el material de anidamiento en cajas con entradas en forma de ranura.

Nest building is important to pair formation in many species of birds, including House Wrens (*Troglodytes aedon*) (Collias and Collias 1984). Nests of House Wrens generally consist of a stick foundation, in which a cup is formed, and a lining of bark, dried grass, hair, feathers, and occasionally snake skin and cellophane. The male builds the nest foundation, generally filling the available cavity space with dry sticks (see Godard 1915), and the female adds the lining (Kendeigh 1941, 1952; McCabe 1965).

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Instructions for building nest boxes suggest that slot entrances enable House Wrens to bring in sticks more readily (U.S. Dept. Interior 1979: 8). In addition, such instructions suggest that for House Wrens, relatively small nest boxes are better than larger ones because wrens will fill the available cavity with sticks. To examine the effects of these parameters on nest building in House Wrens, we provided nest boxes that had either a slot or a hole entrance and that differed in depth. To determine the relative costs of nest building to male and female House Wrens, we measured (1) the mass and number of sticks and the mass of lining brought into each nest, and (2) the duration of nest building.

METHODS

House Wrens were studied in central New Jersey in nest boxes that were put up in either 1983 or 1984 in three old field sites in Somerset and Middlesex counties (see Kennedy [1989] for a description of the study sites). Nest boxes had constant internal basal dimensions (8.9 × 10.2 cm) but differed in depth: "shallow" boxes were 14.0 cm deep and "deep" boxes were 21.6 cm deep. Differences in depth allowed for variation in male nest size without altering the space available for the nest cup and lining. The distance from the box entrance to the floor was 8.9 cm in shallow boxes and 16.5 cm in deep boxes; thus, the maximum possible nest volume in each box size was 808 and 1498 cm^3, respectively. Boxes had either entrance holes of 2.54-cm diameter or entrance holes that had been enlarged to form slots. Each slot had a total length of 6.35 cm, made by cutting an additional 1.9 cm horizontally on each side of the center hole; the portion of a slot that extended from the hole was 1.27 cm in height. Slot-type entrances were intended to ease nest construction while still excluding interspecific nest-site competitors and predators. The four types of boxes (shallow hole, shallow slot, deep hole and deep slot) were distributed randomly among the study sites and among vegetation types within study sites.

In 1986 each nest box was fitted with an insert made from a half-gallon waxed-paper carton in which drainage holes were cut. Nests were built in the inserts. We could remove, weigh and return inserts to boxes without disrupting the integrity of the nests. We measured nest mass to the nearest 0.1 g daily during nest building and through the egg-laying period with a portable electronic balance. We also recorded the time, in days, to build each part of the nest. Male building was defined as the period from the appearance of the first stick until the start of the lining; female building extended from first lining until no more new lining appeared. Only active nests (i.e., nests in which at least one egg was laid) were included in the analyses. After the young had fledged, inserts and nests were removed from boxes, and new inserts were placed in boxes if it was early enough for a second nesting attempt. After removal of inserts, nests were again weighed, and sticks were counted and sorted into two groups: those 6.35 cm or longer (i.e., "long sticks," sticks at least as long as the length of a slot), and those shorter than 6.35 cm ("short sticks").

Nestlings pulled most of the lining materials and some sticks out of nests. Thus, at the end of nesting, lining composition could not be quantified.

House Wrens generally showed two distinct laying peaks in each year. In 1986, wrens began laying on 12 May and there was a gap in starting new clutches from 8–14 June. Nests in which the first egg was laid before 14 June were categorized as early nests; those begun on or after 14 June were called late nests. As clutch size was manipulated as part of an experiment on indeterminate laying (Kennedy and Power 1990), we could not determine whether box size affected clutch size. As manipulated clutch size distributions did not differ between shallow and deep boxes in early nests, however, we did measure incubation and brooding times to determine whether box size affected the length of these times.

Statistical analysis.—To examine whether differences in box size, entrance type or season (early vs. late) had any effects on nest building in wrens, we performed a three-way factorial analysis of variance (ANOVA) using the GLM procedure (SAS Institute 1985) for each of the following dependent variables: total stick mass, maximum mass of sticks added in one day, stick density (the mass of sticks per available volume), total number of sticks, number of long sticks, number of short sticks, number of days to build the stick portion of the nest, total lining mass, number of days to build the lining portion of the nest and total nest mass (sticks plus lining). Stick, lining and nest masses were those obtained during nest building. Sample sizes varied among nest type for some variables because mass was not measured every day at some isolated nests or because an insert was not used at one nest. For comparisons of frequencies we used the log-likelihood ratio test (*G* test) (Sokal and Rohlf 1981).

RESULTS

Entrance type.—Boxes with slot entrances contained heavier nests, due to heavier stick portions of the nest, than did boxes with hole entrances (Tables 1 and 2). Although males did not add significantly more sticks to nests in slot-entrance boxes than to those in hole-entrance boxes (Table 2), they brought different types of sticks to hole and slot nests. Nests in hole-entrance boxes were built almost entirely of *Juniperus* twigs, which were narrower and lighter than the twigs of *Rubus, Rosa,* and various hardwoods used in the slot-entrance boxes (Table 3). Males usually filled more of the cavity (greater density) in slot than in hole nests (Tables 1 and 2). Although there were no differences in time to build the stick portion of the nest between boxes of different entrance types, the maximum mass of sticks added in a single day was greater in slot than in hole nests (Tables 1 and 2).

There were no differences in lining mass or time to add the lining, indicating that entrance type had no effect on female nest building (Tables 1 and 2).

Box size.—Nests in deep boxes were heavier due to greater stick mass, and contained more sticks, particularly long sticks, than nests in shallow boxes (Tables 1 and 2). Density of the stick portion of the nest (mass per

TABLE 1. Nest building in House Wrens. Values shown are mean ± SD.

Nest type	n^a	Total nest mass (g)	Stick mass (g)	Lining mass (g)	Maximum stick mass added/day
Early					
Shallow hole	4	14.8 ± 1.1	10.4 ± 0.6	4.4 ± 1.3	4.2 ± 0.9
Shallow slot	17	25.2 ± 6.6[b]	21.0 ± 6.3	4.2 ± 2.0	7.4 ± 4.1[c]
Deep hole	1	20.7	18.6	2.1	4.9
Deep slot	10	42.0 ± 13.4	37.4 ± 13.7	4.6 ± 2.6	10.1 ± 5.4
Late					
Shallow hole	1	12.4	10.2	2.2	4.1
Shallow slot	5	18.6 ± 4.1	15.4 ± 3.6	3.1 ± 1.2	4.9 ± 0.7
Deep hole	2	14.3 ± 2.1	11.7 ± 1.5	2.6 ± 0.6	2.6 ± 1.0
Deep slot	6	37.7 ± 18.9[e]	33.6 ± 18.5[e]	4.1 ± 1.7[e]	10.5 ± 4.6

[a] n represents the maximum number of nests for which a variable was measured.
[b] $n = 16$; [c] $n = 14$; [d] $n = 1$; [e] $n = 5$.

maximum possible nest volume), however, did not differ between shallow and deep boxes (Tables 1 and 2), suggesting that males generally filled the available cavity with sticks. Time to build the stick portion of the nest did not differ significantly with box size (Table 2).

Nest lining by females was not affected by box size. Neither lining mass nor time to add the lining differed between nests in shallow and deep boxes (Tables 1 and 2).

Season.—Males spent significantly more time building early than late nests; however, there were no differences in the mass or number of sticks added to nests early versus late in the nesting season. Season had no effect on female nest lining (Tables 1 and 2).

Box use.—Box use did not differ with box size (Table 3; 26 of 33 shallow boxes were used vs. 17 of 27 deep boxes; $G = 1.829$, df = 1, $P > 0.10$). Entrance type influenced nest building, however: boxes with slots were more likely to be used for nesting than boxes with holes (Table 3; 33 of 37 vs. 10 of 23, respectively; $G = 14.688$, df = 1, $P < 0.005$). Including dummy nests, wrens used only 12 of 23 hole-entrance nests vs. all 37 slot-entrance nests ($G = 20.16$, df = 1, $P < 0.001$).

We found no evidence that females chose males on the basis of box size; shallow and deep boxes in which males had started a nest were equally likely to be used by females.

Timing of building.—Males and females spent approximately the same number of days adding sticks and lining, respectively (males 6.63 ± 2.55 d, $n = 43$; females 6.41 ± 2.70 d, $n = 46$; Wilcoxon paired-sample test [$n = 43$], $P > 0.10$). This probably does not represent an equal daily effort on the part of each sex, however. Limited observations during nest building suggested that males brought sticks one-at-a-time; thus each stick probably represented a single visit. The mean (± SD) total number of sticks in boxes was 318 (± 216, $n = 44$), and ranged from 41 at a shallow late nest to 970 at a deep early nest. The daily changes in stick mass that

TABLE 1. Continued.

Density (mg/cm³)	Total no. of sticks	No. of short sticks	No. of long sticks	No. of days to add sticks	No. of days to add lining
12.9 ± 0.8	113 ± 37	86 ± 30	27 ± 13	8.5 ± 2.9	6.0 ± 1.2
25.8 ± 8.0[b]	289 ± 156[b]	221 ± 120	68 ± 46	6.4 ± 2.3	7.5 ± 3.5
12.4	349	247	102	10	5.0
25.0 ± 9.1	496 ± 243	319 ± 198	177 ± 89	7.2 ± 2.0	6.7 ± 2.5
12.4	162	124	38	3	7
18.6 ± 4.1	178 ± 79	115 ± 49	63 ± 42	4.8 ± 2.1	6.2 ± 1.9
14.3 ± 2.1	256[d]	174[d]	82[d]	7.0 ± 0	5.0 ± 0
37.7 ± 18.9[e]	460 ± 264	333 ± 218	127 ± 53	6.2 ± 1.7[e]	5.2 ± 1.7[e]

we recorded indicated that male wrens did not add constant masses of sticks on successive days.

Incubation and nestling periods.—Among early nests, the incubation period (the time from the laying of the last egg to the first hatching day) was significantly longer in shallow boxes than in deep ones ($\bar{x} \pm$ SD, 12.6 ± 0.60 d [n = 22] vs. 12.1 ± 0.54 [n = 11]; $t = 2.22$, df = 31, $P < 0.05$). The nestling period (the time from hatching to fledging) did not differ between shallow and deep boxes (16.3 ± 1.2 vs. 16.3 ± 0.8 d), however.

DISCUSSION

Entrance type.—Male wrens did not pick boxes on the basis of box depth. Males were more likely to select boxes with a slot rather than a hole entrance, however. Entrance dimensions should be more important to males than to females due to the differences in the type of materials brought to the nest. Males may be discouraged by the difficulty of fitting sticks through a small hole (Barrows 1912:673–674) or the time and effort required in filling a large cavity with small sticks. Female House Wrens bring small, flexible lining materials that can easily fit through narrow holes, and are probably less influenced by nest entrance size and shape than males.

Our results suggest that males initially chose the nest sites, probably based on entrance dimensions, and that females then selected among the males.

Box size.—Male nest-building effort differed significantly between deep and shallow boxes, while female effort did not differ between boxes. Thus, nest-building costs to male House Wrens were cavity-size dependent while costs to females were relatively fixed.

Although all boxes in this study had the same basal area, basal area did not appear to limit wren nest cup size. McCabe (1965) found that wrens nesting in cans with a 15.5 cm diameter (volume 2839 cm³) built

TABLE 2. F values and levels of statistical significance based on the results of a factorial analysis of variance (ANOVA) of box size, entrance type and season (type-III sums of squares [SAS Institute 1985]). No significant interaction effects were found.

	Total nest mass	Stick mass	Lining mass	Maximum stick mass added/day	Density	Total no. of sticks	No. of short sticks	No. of long sticks	No. of days to add sticks	No. of days to add lining
Box size	4.87*	5.05*	0.02 ns	0.90 ns	0.04 ns	4.46*	2.88 ns	5.83*	3.33 ns	0.82 ns
Entrance type	9.61**	8.26**	1.58 ns	4.61*	8.94**	1.95 ns	1.32 ns	2.33 ns	0.85 ns	0.24 ns
Season	1.00 ns	0.71 ns	0.72 ns	0.32 ns	0.84 ns	0.24 ns	0.16 ns	0.28 ns	6.96*	0.11 ns

* = $P < 0.05$; ** = $P < 0.01$; ns = $P > 0.05$.

TABLE 3. Box use and type of sticks added by male House Wrens at boxes differing in size and entrance type.[a]

Box size	Entrance type	Use	Type of sticks
Shallow	hole	7/13	*Juniperus, Rubus*
Shallow	slot	19/20	*Rubus, Rosa,* hardwood spp.
Deep	hole	3/10	*Juniperus, Vitus* bark
Deep	slot	14/17	*Rubus,* hardwood spp., *Juniperus*

[a] Only nests in which at least one egg was laid are included. Box use is indicated by the number of boxes with active nests per number of boxes available. Some boxes were used for both early and late nests. Stick types are listed in order of frequency of occurrence.

nests that on average contained 121 ± 5.1 g of sticks (n = 52), significantly larger than the masses found in our nests (32.4 ± 4.0 g in deep boxes and 18.0 ± 1.3 g in shallow boxes). In spite of large differences in the average amount of sticks brought by males, however, the average mass of lining brought by females did not differ among nests of different sizes (3.6 ± 2.04, n = 26 in McCabe's [1965] study vs. 4.0 ± 2.03, n = 45 in our study; t = 0.80, df = 69, $P > 0.20$). These findings suggested that wren nest cups were fairly standard in size, regardless of the size of the male portion of the nest.

Season.—McCabe (1965) found that males that acquired mates early in the breeding period usually built smaller nests than those that obtained mates later. We found, however, that neither males nor females added more material to late nests than to those started before 14 June. Ambient temperatures are more variable during the early nesting period (Kendeigh 1952), and a heavier nest and lining may be important for more efficient thermoregulation during that time. Although Kendeigh (1952:18–19) found that the nest lining was mostly completed by the females within 2 d of high activity (170 visits per day was the average maximum number observed by Kendeigh), we found that females generally continued to add lining, especially feathers, during egg laying, and some even added through part of the incubation period.

Incubation period.—Incubation time was, on average, one-half day shorter in deep than in shallow boxes. This may represent an advantage to females nesting in large cavities. Baltz and Thompson (1988) found an increased incubation period of one-half day in House Wrens that incubated artificially enlarged clutches, and they suggested that a longer incubation time may be a cost to females. We found no effect of box size on hatching or fledging success, suggesting that, in this population, a one-half day increase in incubation did not have a deleterious effect on reproductive success.

Timing of building.—Kendeigh (1952:16) found that males made an average of 29 daily nest visits during "ordinary activity," and made more than 100 daily visits when actively nest building. In our study, most male wrens had days of relatively high activity interspersed with days of little or no nest-building activity. Kendeigh (1952:17) found that the arrival of a female on a male's territory resulted in increased male activity, as measured by visits to the nest, that continued for some time even after the female left.

Female wrens may make as many daily visits to a nest as males. Time budgets may be more limiting for males during nest construction, however, because they must also sing and defend territories. Competition for territory in House Wrens involves singing but also commonly involves chasing and actual combat (Belles-Isles and Picman 1987, Kendeigh 1941). Furthermore, although male nest-building activity generally centers around a single box at which the nest "is usually best-formed and has the largest number of sticks," males often claim and defend several additional nest sites, known as "dummy nests" (Kendeigh 1941:24). Dummy nests usually contain only a very few sticks or, in some cases, only a single stick (Kendeigh 1941:24), but their establishment and defense represent additional costs to males that females do not incur.

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