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AN EXPERIMENTAL TEST OF THE FUNCTION OF STICKS IN THE NESTS OF HOUSE WRENS[1]

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Key words: House Wren; nest building; sex roles in nest building; nesting success; Troglodytes aedon.

Males of several species of wrens (Troglodytidae) participate to varying degrees in nest building, some even building multiple nests (Kendeigh 1941, Verner 1965, Collias and Collias 1984, Kennedy and White 1992). The Northern House Wren (*Troglodytes aedon*) is a monomorphic, insectivorous, secondary cavity nesting species which is seasonally monogamous although polygyny does occur (Kendeigh 1941, Drilling and Thompson 1988, Johnson and Kermott 1991). Male House Wrens build multiple nests within their territories by placing sticks into several cavities (Kendeigh 1941, McCabe 1965, Finch 1989), while one cavity is the focus of the male's attention and receives the most sticks (Kendeigh 1941, Belles-Isles and Picman 1986). Soon after a female arrives on the male's territory she constructs a soft nest of rootlets, grass, and feathers on top of the stick foundation into which she deposits her eggs (Kendeigh 1941, Kennedy and White 1992). Although females insert some sticks into cavities (Kendeigh 1941, McCabe 1965), it is the male that expends the most effort filling nesting cavities with sticks (Kendeigh 1941, Kennedy and White 1992).

Two hypotheses advanced (Kendeigh 1941) to explain the function of this behavior were territorial claim and female choice. Since competition for suitable nesting sites may be high for cavity-nesting species (Yahner 1983/1984, Brawn and Balda 1988, Gustafsson 1988), by placing sticks into cavities first, early arriving males may outcompete later arrivals for a favorable nest site. In many monomorphic species, males may be subject to stronger sexual selection which may manifest itself in behavioral rather than morphological consequences (Andersson 1994). Females may therefore select males based on the extent to which the stick foundation is completed (Kendeigh 1941), and may evaluate a male's commitment to her and the nest site similar to the Black Wheatear, *Oenanthe leucura* (Moreno et al. 1994), perhaps reducing her chances of being a secondary female if mated with a polygynous male. The extent to which the sticks serve a specific function with regard to the nest structure itself has not been tested.

By preventing males from filling treatment nest boxes with sticks, I tested two hypotheses. First, if filling a nest box with sticks by males is necessary for courtship and mating, then stick removal from boxes should preclude pair-bond formation. Second, if having a stick foundation enhances fledgling success in some way, than pairs with sticks removed should be less successful in rearing and fledging young.

METHODS

I studied an unbanded population of House Wrens at the Edmund Niles Huyck Preserve and Biological Research Station on the Helderburg Plateau, southwest Albany County, New York (elev. 370–500m, 42°10′N, 74°10′W). I used 70 nest boxes during the summers of 1992 and 1993 and 40 in 1994. Nest boxes were spaced at least one acre apart in preferred wren habitat (Parren 1991). The boxes measured 10 × 14 × 20 cm internally, with an entrance hole 3 cm. in diameter and were painted either dark brown or forest green. Boxes were attached to a tree or metal post with the entrance hole approximately 1.5 m. above the ground and opened from the front to facilitate nest examination and stick removal.

Nest boxes were randomly assigned each year to treatment or control groups prior to the arrival of wrens

TABLE 1.   Measure of reproductive output of House Wrens nesting in boxes with sticks removed and control boxes. Shown are means ± SD (number of nests). All $P > 0.10$.

Measure	Treatment		t
	Sticks removed	Control	
No. eggs laid	5.7 ± 1.6 (21)	5.4 ± 1.3 (25)	0.87
No. young fledged (all nests)	4.0 ± 2.8 (21)	2.8 ± 2.8 (25)	1.55
No young fledged (successful nests)	5.6 ± 1.2 (15)	5.3 ± 1.4 (13)	0.85

in the spring. All sticks placed in treatment boxes were removed daily and sometimes twice per day to insure that very few if any sticks were in treatment boxes at any given time. Stick removal from treatment boxes began on the second day that sticks were observed to have been placed into a nest box. Control boxes were also opened and closed daily but the sticks were not disturbed. Stick removal was terminated when the female began to build the soft portion of the nest. The number of sticks removed from treatment boxes and present in control boxes were determined as was the weight of the soft portion of all nests. Sticks removed were placed into individual plastic bags with the date, location, weight, and number of sticks recorded.

All boxes were visited daily throughout the nesting seasons to monitor the number of eggs, hatchlings, and fledglings as well as the duration of each of the nesting stages. I defined nesting stages as follows:

Stage 1: Period from when a wren first placed sticks into a nest box until the time when the first soft lining appeared.
Stage 2: Period from when the first soft lining appeared until the first egg was laid.
Stage 3: Period from when the first egg was laid until the first egg hatched.
Stage 4: Period from the appearance of the first hatchling until the first offspring fledged.

RESULTS

Males placed sticks in 77 of 180 nest boxes available over the 3 year period, of which 42 were control boxes and 35 were treatment boxes. Females built the soft nest structure in 30 of the 42 control boxes (71%) and in 24 of the 35 treatment boxes (69%), suggesting that treatment and control males did not differ in their ability to attract a mate ($\chi^2 = 0.01$, df = 1, $P > .90$).

Females laid eggs in 25 of the 30 control boxes (83%) and in 21 of the 24 treatment boxes (87%). The number of eggs laid per nest did not differ between experimental

and control females ($t = 0.87$, df = 44, $P > .45$, Table 1).

Treatment and control pairs did not differ in the number of young fledged (85 vs. 69, respectively, $t = 1.55$, df = 44, $P = 0.12$, Table 1). With regard to successful nests only (i.e., those that fledged at least one young), treatment females fledged as many young as control females (Table 1).

The mean day of nest initiation (day first egg is laid) for both treatment and controls were within one day of each other all 3 years, suggesting both treatment and control nests were active each year at the same time. I found no differences in the duration of any nesting stage between control and treatment boxes (Table 2). The number of sticks removed from treatment boxes (mean ± SD = 1,158 ± 564, $n = 20$ boxes) differed significantly from the number of sticks in control boxes (643 ± 250, $n = 17$ boxes, $t = 4.06$, df = 35, $P < 0.001$). I observed no significant difference between control and treatment female nest weights (treatment mean ± SD = 25.00 ± 11.70 g, $n = 12$; control mean = 27.90 ± 17.43 g, $n = 15$; $t = -0.48$, df = 25, $P > 0.60$). The percentage of nests lost (due to all causes) was higher for control boxes (56%) than treatment boxes (33%), although not significantly so ($\chi^2 = 0.90$, df = 1, $P = 0.34$).

DISCUSSION

Removing sticks from nest boxes did not prevent males from acquiring mates, effect the duration of nesting stages, reduce the number of young fledged or increase nest loss rate. These results suggest that filling nest boxes with sticks by males is not a prerequisite for successfully attracting a female, nor are they necessary for successfully rearing young in the House Wren. Because I removed sticks daily and sometimes twice per day, females had little opportunity to observe sticks in treatment boxes. If female assessment of male quality was based on the number of sticks in a nest box, treat-

TABLE 2.   Nest stage duration of House Wrens in boxes with sticks removed and control boxes measured in days. Shown are means ± SD (number of nests). All $P > 0.17$.

Measure	Treatment		t
	Sticks removed	Control	
Stage 1 (first stick to first soft material)	15.0 ± 6.6 (19)	12.0 ± 8.4 (25)	1.41
Stage 2 (first soft material to first egg)	6.0 ± 3.5 (20)	6.0 ± 2.9 (21)	0.03
Stage 3 (first egg to first hatchling)	19.0 ± 3.1 (15)	18.0 ± 2.0 (17)	0.29
Stage 4 (first hatchling to first fledgling)	16.0 ± 4.3 (14)	15.0 ± 4.8 (11)	0.96

ment males should have had lower success in acquiring mates than control males because there were few if any sticks in treatment boxes, whereas there were on average 643 sticks in control boxes. Furthermore, stick removal did not affect nesting success. In fact, treatment pairs laid more eggs and fledged more young on average than did controls although the difference was not significant. Stick removal did not significantly alter the duration of any of the four nesting stages. The slight delay in stage one for treatment pairs can perhaps be accounted for by the female's commitment to carrying sticks to the nest box herself prior to her building the soft portion of the nest.

Stick removal did not affect the ability of treatment females to build "her" soft portion of the nest; treatment and control nests did not differ by weight or in the time that females took to build them. Although treatment nests were nearer to the bottom of the nest box due to stick removal, fledging was not delayed. This makes it unlikely that sticks function to facilitate fledging from deep cavities. Finally, predation, which is known to be responsible for a high percentage of House Wren nest failures (Finch 1990), occurred in both treatment and control boxes during this study. Since there were no significant differences between treatment and control boxes with regard to predator success, the sticks appear not to serve an anti-predator function in nest boxes.

Since the number of sticks accumulated in boxes seems not to affect nesting success, we are forced to examine other possible functions for this behavior. Ectoparasites can play a significant role in the success or failure of cavity nesting birds (Møller 1989). Perhaps sticks serve to reduce nestling ectoparasite load as do feathers in Tree Swallow (*Tachycineta bicolor*) nests (Winkler 1993), by providing an alternative location for parasites thereby diluting their effect on the nestlings. Alternatively, the sticks may help to regulate nest box temperature and acting as insulation, may reduce heat loss by nestlings in large cavities which may be important to their developmental rate (Kendeigh 1963, 1972). Because there is a high degree of variation regarding the number of sticks placed in a nest box by House Wrens (T. Alworth, pers. observ.), both of these hypotheses could be tested by comparing incubating temperatures and/or parasite loads between unmanipulated nests that contain few sticks with those containing many sticks.

During the course of this study, I observed females carrying the majority of sticks to nest boxes prior to her building the soft portion of the nest. Since stick carrying behavior is most often attributed to males only, this observation was surprising. I am currently investigating the female's role with regard to carrying sticks to the nest which may be similar to that of Rock Wrens (*Salpinctes obsoletus*) in which females participate in the construction of a stone foundation (Merola 1995). Perhaps the female's stick carrying serves as the culmination of courtship and therefore the act of stick carrying itself, and not their presence in the nest cavity, may be important. Clearly, we must verify the role of both sexes regarding stick carrying behavior if we are going to fully understand its function.

In summary, removing sticks daily from the nests of House Wrens had little effect on pair-bond formation, nesting stage duration, number of eggs laid or young fledged, therefore their function remains unclear.

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DIVING PATTERN AND STOMACH TEMPERATURES OF FORAGING KING CORMORANTS AT SUBANTARCTIC MACQUARIE ISLAND[1]

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Key words: King Cormorant; diving; stomach temperature; food ingestion.

Logging stomach temperature in marine endotherms has enabled the determination of when and how much food has been ingested by free-ranging seabirds (Weimerskirch and Wilson 1992, Wilson et al. 1992, Grémillet and Plös 1994, Pütz and Bost 1994). While considerable errors in mass estimates caused by factors such as position of the loggers and activity of the animal can occur using this technique, the timing of prey ingestion can generally be determined accurately (Wilson et al. 1995).

We simultaneously recorded the diving depth and stomach temperatures of free-ranging King Cormorants (Phalacrocorax albiventer) using micro data loggers with the goal of quantifying the variability between the top and bottom stomach temperatures and comparing methods to estimate meal mass in free-ranging seabirds. Here we report on the advantage of using two temperature sensors on the top and bottom of the loggers, and the problems in determining the feeding activities of seabirds from their stomach temperature.

MATERIALS AND METHODS

The study was conducted at the Handspike Point colony on subantarctic Macquarie Island (54°30′S, 158° 57′E) in January 1994. Two micro data loggers (0.5

Mbytes memory size, Little Leonardo Co. Ltd., Tokyo) were used for each bird: a time depth logger (TDL) and a stomach temperature logger (STL). The TDL had a cylindrical shape, 75 mm long and 19 mm in diameter, with a domed top and weighed 35 g including battery. It included a pressure sensor which measured depth with accuracy of 1.0 m and resolution of 0.1m. The STL had a cylindrical shape, 90 mm long and 19 mm in diameter, with a domed top and bottom and weighed 35 g including battery. Single sensors at the top and bottom of the STL each measured temperature with an accuracy of 0.1°C. Both loggers were programmed to sample temperature or depth every 6 sec. TDLs were attached on the back of the King Cormorants with cable ties and quick-set epoxy glue. Birds were then induced to swallow STLs. Both TDLs and STLs were deployed on five breeding males that were then released at the colony. Three birds were recaptured after a single foraging trip and the loggers were successfully recovered. The other two birds returned to the colony without their STLs. We believe they were regurgitated earlier, and only their TDLs were recovered. At the time of retrieving the loggers, stomach regurgitations were collected; details of the collection and analysis of regurgitations are described in Kato et al. (1996).

Data from the loggers were downloaded onto computer for analysis. For each dive deeper than 1 m, maximum depth, duration, bottom time (time spent at depth greater than 85% of maximum dive depth), descent rate, ascent rate, and surface duration were determined. Stomach temperature drops often coincided with diving events (Fig. 1a). For each stomach temperature drop that exceeded 0.2°C (because the