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EFFECT OF NEST-SITE SUPPLEMENTATION ON POLYGYNOUS BEHAVIOR IN THE HOUSE WREN (*TROGLODYTES AEDON*)[1]

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Several recent studies have documented repeated incidents of polygyny in populations of secondary-cavity nesting birds provided with an abundance of nest boxes (Dhondt 1987, Marks et al. 1989, Korpimäki 1989, Pinxten et al. 1989, Alatalo and Lundberg 1990, Petit 1991, and references in each). During a study of House Wrens (*Troglodytes aedon*) in Wyoming, we found that over half of males with at least two nest boxes on their territories became polygynous. Price (1986) and Quinn (1989) have also recorded high rates of polygyny among box-nesting House Wrens in Illinois and Alberta, respectively. In the Wyoming population, polygyny appeared to be costly to second-mated females because they received less parental assistance from mates and fledged fewer young than monogamous or primary females (in prep.). Reduced reproductive success for second-mated females has been documented in other box-nesting species including Pied Flycatchers (*Ficedula hypoleuca*; Alatalo et al. 1981, Stenmark et al. 1988), Blue Tits (*Parus caeruleus*; Dhondt 1987), Boreal (Tengmalm's) Owls (*Aegolius funereus*; Solheim 1983, Carlsson et al. 1987, Korpimäki 1991), European Starlings (*Sturnus vulgaris*; Pinxten and Eens 1990), Prothonotary Warblers (*Protonotaria citrea*; Petit 1991), and House Sparrows (*Passer domesticus*; Veiga 1990).

To explain the occurrence of polygyny in these species, most researchers have invoked one of several formal models that outline conditions under which polygyny, although costly to fitness, can still be an adaptive choice made by females (Searcy and Yasukawa 1989). However, these models assume that polygyny evolved in situations where females were routinely faced with a choice of paired and unpaired mates. Alatalo and Lundberg (1984) cautioned that if in the "natural situation" the abundance and dispersion of suitable cavities is such that males rarely control more than one nest site, there may be little selection on females to identify and consider the pairing status of a potential mate. Thus, the seemingly maladaptive choice of polygyny made by females in box-nesting populations could be an artifact of providing males with a surplus of high quality nest sites. Alatalo and Lundberg (1984) rejected this hypothesis for Pied Flycatchers by showing that similar proportions of males in areas with and without nest boxes attempted to attract second mates. In contrast, Petit (1991) reported that in the natural situation male Prothonotary Warblers very rarely have access to more than one natural nest cavity and polygyny is extremely rare. She too suggested that polygyny may occur much more frequently in this species when males have a surplus of nest boxes because females are "evolutionarily naive" to the costs of polygyny. This hypothesis was not considered in the other studies cited above with the exception of Marks et al. (1989; see also Korpimäki 1991:44).

The purpose of this study was to determine whether the occurrence of polygyny among box-nesting House Wrens was an artifact of allowing males access to more than one nest box per territory. We asked if and how frequently in the natural situation female House Wrens pair polygynously, and how frequently paired males attempt to attract second mates. We compare these data to similar data gathered when we provided each male with several boxes per territory. Because the frequency of polygyny has not been documented for any naturally-nesting population of House Wrens, we felt that this study was critical prior to testing formal models for the occurrence of polygyny in this species.

METHODS

We studied wrens on the Quarter-circle A and Gallatin Ranches near Big Horn, Sheridan Co., Wyoming (44° 40′ N, 106° 56′ W; 1,310 m). Wrens were observed from their arrival on site in early May until early August when all or most nesting attempts had been completed. Wrens occupied wooded areas, mostly of box elder (*Acer negundo*), along the Little Goose Creek and its tributaries which flowed through pastures and hayfields. In 1985 and 1986, we erected 2–3 boxes, 25–40 m apart, in each of 10–15 locations prior to the return of wrens in spring. Boxes were removed and washed

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out at the end of each season. We did not erect boxes on the study site in 1987 to allow observations of males and females with access only to natural cavities. All but one of the males in this study were individually marked with colored leg bands prior to observations. Most females were unmarked.

Frequency of polygyny. We documented the frequency of polygyny among a subset of 15 males provided with boxes (hereafter "Box males"), and 31 males that had access only natural cavities ("NC males"). Males chosen for this comparison were those who began first nesting attempts early enough in the season to have potentially attracted a second mate. First mates of all 46 males had at least completed their incubation stage, the stage during which most polygynous males obtained second mates, before the last pairing of the season was observed. In addition, the Box males included this analysis were males who controlled at least one extra box within their territorial space. Some males had three boxes on their territories but all males appeared to focus their activity around only one of the extra boxes. Males were observed for 20–60 min every one to four days throughout their incubation and nestling stages. Polygyny was easily detected because males with two mates regularly flew back and forth between nests, especially before the second mate began incubating.

Effort at attracting second mates. Our initial study of box-nesting wrens strongly suggested that males use song to attract mates (Johnson and Kermott 1991). After their first mates began incubating, most males repeatedly moved near one of the unoccupied boxes on their territory and sang loud, long bouts of song in a manner similar to that when unpaired. Males who attracted a second mate immediately ceased this "advertising." Males rarely sang elsewhere when away from the first mate's nest, probably because song plays a limited role in regular territory defence. Therefore, to gauge a male's effort in attracting a second mate, we documented the amount of song he sang away from his first mate's nest, and the proportion of that song sung near an unoccupied cavity.

We compared song output for six Box and 17 NC males. We limit comparisons to the 14 day incubation stage. Males do not incubate and all males should therefore have approximately equal amounts of time during this stage to advertise for second mates. Data for Box males were gathered from the day that the penultimate egg was laid (when females usually start regular incubation) to the day before eggs hatched. Because we could not examine contents of natural cavities, we started observations on NC pairs during the egg-laying stage to determine the day that the female began regular bouts of incubation, and continued gathering data to the day before adults began regular food deliveries to the nest. Birds were observed between 06:00 and 10:00 for a predetermined length of time of between 20 and 50 min (usually 30 or 45 min) on as many days as possible.

We defined the "nest area" as the area within 10 m of the first mate's nest. Each male had one or two preferred perches in this area from which he interacted with his mate. Using a stopwatch and hand-held tape recorder, we noted the times that the male moved more than 10 m or in or out of the nest area, the number of songs he had sung at the previous location, his new location, and his current activity. We counted all songs sung away from the nest area, and calculated the proportion of those songs sung near an unoccupied cavity (i.e., within about 10 m of the cavity; again, most males had preferred perches near these cavities). Vegetation was patchily distributed on all territories which greatly assisted in describing male location.

TABLE 1. Variation in effort and success at attracting second mates by males that were provided with at least two nest boxes on their territories. Shown are total songs/hr sung away from the first mate's nest area and, in parentheses, the number and percent of those songs sung near an unoccupied box.

Male	Days/min observed	Total songs/hr (near box)	Attempts/ succeeds in becoming polygynous?
OG-644	9/264	92 (73–79%)	Yes/No
LB-610	8/235	146 (120–82%)	Yes/No
OR-643	5/136	151 (119–78%)	Yes/Yes
MB-604[a]	2/60	166 (166–100%)	Yes/Yes
Bw-710	12/360	183 (172–94%)	Yes/No
LG-703	6/175	32 (19–59%)	No/No

[a] Data for 1986 (see data for same male in Table 2).

RESULTS

Three of 31 (9.6%) NC males attracted second mates. However, polygyny occurred more frequently among Box males (8 of 15 [53.3%] males; Fisher's exact test $P = 0.002$).

Among males whose behavior was observed in detail, five of six (83%) Box males and eight of 17 (47%) NC males appeared to make consistent attempts at attracting second mates (Tables 1, 2). These males had relatively high song outputs from one or two locations on their territories. Of the eight NC males, we observed all but Male YO-865 investigate or build in cavities at these locations. We assume from his behavior that Male YO-865 had access to a second cavity where he was singing. Males do not routinely enter their extra cavities so our failure to detect some cavities was not unexpected. Males LF-UB and DN-892 advertised for second mates immediately after cavities were vacated by neighboring wrens. Seven other NC males (41%) appeared to make no attempt at polygyny at any point during the incubation stage. These males had relatively low song outputs and did not sing consistently from any location(s) on their territories. The two remaining males, RO-888 and SM-909, made weak efforts, if any, at becoming polygynous. These males had low song output, but did sing consistently at one and three locations in their territories, respectively. We do not know if there were cavities at any of these locations.

Box and NC males that consistently advertised for second mates did not differ in mean song output (Table 3). If we include in analyses the two males who may have made weak attempts at polygyny (RO-888 and SM-909), mean song output for NC males is lower but still not significantly different from the mean for Box males.

TABLE 2. Variation in effort at attracting second mates made by males who had access only to natural cavity nest sites. For each male we note whether he sang in the same location(s) when away from his first mate's nest area, and whether we observed the male entering a cavity at these locations. We then indicate songs/hr sung away from the first mate's nest area and, in parentheses, the number and percent of those songs sung in locations that we knew or suspected were near unoccupied nest sites. Finally, we indicate whether we considered the male to have made a consistent attempt at attracting a second mate. None of these males became polygynous.

Male	Days/min observed	Sings in same location(s)? (how many)	Cavity present?	Total songs/hr (near cavity)	Attempts polygyny?
BW-853	12/373	Yes (1)	Yes	49 (35–71%)	Yes
Hu-893	8/400	Yes (1)	Yes	104 (91–88%)	Yes
CS-706	9/387	Yes (2)	Yes	115 (115–100%)	Yes
EG-881	7/322	Yes (2)	Yes	114 (110–96%)	Yes
PT-910	13/597	Yes (1)	Yes	274 (274–100%)	Yes
YO-865	9/405	Yes (1)	?	98 (86–88%)	Yes
LF-UB[a]	4/185	No	—	24	No
	9/428	Yes (2)	Yes	102[b] (95–93%[b])	Yes
DN-892[a]	9/413	No	—	15	No
	2/90	Yes (1)	Yes	215 (187–87%)	Yes
RO-888	13/566	Yes (1)	?	16 (11–69%)	?
SM-909	13-593	Yes (3)	?	33 (30–91%)	?
Br-716	5/200	No	—	0	No
FX-879	11/443	No	—	0	No
BR-858	11/279	No	—	0	No
RF-885	11/508	No	—	7	No
MB-604[c]	11/358	No	—	7	No
RW-918	13/588	No	—	14	No
LT-882	8/240	No	—	18	No

[a] Males switched behavior abruptly when cavities become available (see text).
[b] These are substantial underestimates because ambient noise made accurate counts of songs near peripheral cavities impossible.
[c] Data for 1987 (see footnote to Table 1).

DISCUSSION

Polygyny did occur when males had access only to natural cavities, albeit at a lower rate than when males had two or more nest boxes on their territories. Because Box and NC males were observed in different years, the observed differences in rates of polygyny and male behavior may have resulted from between-year differences in population size or sex ratio. However, the lower rate of polygyny among NC males is probably attributable, at least in part, to a lack of suitable extra nest sites on some territories. Judging from the vegetation on territories (e.g., number of dead trees and holes therein), we estimated that about 25% of the 31 NC males had territories without extra nest sites. Polygyny may also occur less frequently in the natural situation because females consider boxes to be of higher quality than most natural cavities, perhaps of sufficient quality to offset the costs of polygyny. Females may have preferred boxes for several reasons. For example, boxes did not contain old nests, and their entrances were small (2.5–3.1 cm) which may have made the nest within less susceptible to some predators and/or interference from larger cavity-nesting species. The fact that "floater" male wrens try to usurp territories with boxes more frequently than territories with natural cavities suggests that males consider boxes to be of higher quality (Johnson and Kermott 1990).

Our results also indicate that in the natural situation, unpaired females would routinely encounter paired males attempting to become polygynous. About half of males on territories without nest boxes attempted to attract second mates to unoccupied cavities. Some males may not have advertised for a second mate be-

TABLE 3. Comparison of male effort in advertising for a second mate as measured by total song output (mean ± SD songs/hr) away from the first mate's nest area, and song output specifically near an unoccupied box or natural cavity. Data are for males that we considered to make consistent attempts at becoming polygynous (first five males in Table 1 versus first six males of Table 2 and Male DN-892 after he had access to a cavity).

	Type of nest site			
	Box	Natural	t_{10}	P
Total songs/hr	148 ± 34	138 ± 78	0.24	0.81
Songs near nest site	130 ± 40	128 ± 79	0.05	0.96

cause their territories contained only one suitable cavity (e.g., two males had only one tree on their territories which was occupied by their first mate).

In conclusion, although supplying males with a surplus of nest boxes may increase the frequency of polygyny among House Wrens in this population, the occurrence of polygyny does not result solely from the presence of boxes. Males without access to boxes also attract second mates. We also reject the hypothesis that when males are given extra nest boxes, females "mistakenly" choose polygyny (i.e., incur fitness costs) because normally there has been little selection on females to consider the pairing status of potential mates. Because nearly half of paired males on territories without boxes have access to extra cavities and attempt to attract mates to them, past selection should have favored females who considered male pairing status and the cost of polygyny when choosing mates.

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