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# The Enigma of Multiple Nest Building by Male Marsh Wrens

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Male Marsh Wrens (*Cistothorus palustris*) build multiple domed "dummy" nests on their territories, which collectively comprise the "courting centers." Males sing and display to females from these nests (Welter 1935). Females usually build the "breeding" nests in which eggs are laid (Welter 1935). Male Marsh Wrens continue to build nests even after females have begun to incubate. Marsh Wrens frequently mate polygynously, although the proportion of polygynously mated males in a population varies from marsh to marsh (Verner 1963, Leonard and Picman 1987a). Normally the number of nests a male builds far exceeds the number of females attracted to the territory. It has been proposed that male wrens build multiple nests to attract females (Verner and Engelsen 1970, Garson 1980). According to this sexual-selection hypothesis, females gain information about male vigor and territory quality, or both, from the number of nests a male is able to build.

Another possible explanation of the significance of multiple nests is that they function as decoys to reduce predation on breeding nests (Shufeldt 1926, Robinson 1985). This "predator avoidance" hypothesis makes a prediction similar to the "sexual selection" hypothesis, in that females should select male territories with many nests to reduce predation on their clutches. The more dummy nests that surround the breeding nest, the greater the chance that a predator will find an empty nest and leave the general area before discovering the breeding nest (Robinson 1985). Breeding nests near large numbers of dummy nests should therefore be more successful in avoiding predation.

In addition to the absolute number of dummy nests on a territory, the distribution of dummy nests may also contribute to a female's choice of mates or territories, and the likelihood that predators will find the breeding nest.

Tests of the two hypotheses for male nest building have produced ambiguous results. Studies by Verner and Engelsen (1970) and Tintle (1982) showed that male pairing success was correlated with the number and density of dummy nests built by a male over the season. However, Leonard and Picman (1987b) found no evidence that the number or density of dummy nests, or the proportion of time males spent building nests, affected the number of females that settled on territories. Leonard and Picman (1987b) did find that breeding nests were more successful when they were near larger clusters of dummy nests.

I attempted to investigate further the sexual selection and predator avoidance hypotheses for multiple nest building by male Marsh Wrens. I tested the predictions that the number, location, and density of dummy nests should affect female settlement and the success of breeding nests. If female Marsh Wrens prefer males that build more dummy nests, but the dummy nests provide no predator protection, then the sexual selection hypothesis is supported. If females do not prefer males that build more nests, but dummy nests do provide protection, then the predation hypothesis is supported. The two hypotheses cannot be distinguished if females prefer males with more nests, and the dummy nests provide predator protection. Finally, if neither condition is met, then neither hypothesis is supported.

I conducted this study from 1 May to 13 July 1989, in a 14-ha section of a large cattail (*Typha* sp.) marsh near Seeley's Bay in eastern Ontario. Male Marsh Wrens built nests along the edges of a large creek that ran through the middle of the marsh. Estimates of territory boundaries were based on observations of territorial display and defense by the unbanded Marsh Wrens. *Courting centers* were defined as the area of the convex polygon that incorporated dummy nests on a male's territory where males sang and displayed. Male territories were separated by distances >30 m, and dummy nests in courting centers were on average <5 m apart. I was confident that the nests in courting centers belonged to one male. One instance when a dummy nest was farther than 30 m from any breeding or dummy nest was considered not to belong to a courting center and was excluded from the analyses.

I checked 30 Marsh Wren territories four to five times a week for the presence of nests. Most nests were found when males or females began construction. I could not tell whether a completed nest (when the external structure, including the dome, was intact) was a breeding or a dummy nest by any obvious physical differences in the external structure. I examined the contents of all completed nests and recorded the presence or absence of eggs or nestlings. Because all clutches were found when the first or second egg of the clutch was laid in the breeding nest (all completed clutches had six eggs, $n = 17$), I was confident that I located all nests that were used for breeding among all the nests observed. Nestlings were assumed to have fledged if they were present 11 days after hatching, but absent on any subsequent day (following Leonard and Picman 1987a). Predation of nests was assumed to have occurred if all the eggs disappeared simultaneously or all the young disappeared before they were 12 days old. If the nest opening was enlarged and the nest dislodged, I assumed it was destroyed by mammals (Leonard and Picman 1987b). If the nest contents disappeared but the nest was undisturbed, it was considered preyed upon by either snakes or conspecifics (Leonard and Picman 1987b). There were no cases of partial nest losses.

I measured the distances between all nests within a territory to the nearest 10 cm and plotted nest positions on a map of the study area. The distances between nests that were completed when females settled on territories (i.e. when an egg was first detected in the breeding nest) were then used to test the predictions of the sexual-selection and predator-avoidance hypotheses. I used a particular distance between two nests only once in an analysis. Data were analyzed using the statistical package for the social sciences (Nie 1988). All means are reported ±SE. All *P*s are one-tailed. Parametric tests were used where sample sizes and distribution of data warranted, otherwise nonparametric tests were applied.

*Dummy nests did not attract females.*—The number of dummy nests per territory did not appear to be important to females choosing mates. Seventeen of 30 males attracted a female to breed on their territories, although no male attracted more than one female.

TABLE 1. Comparison of the number ($\bar{x}$ ± SE) of dummy nests surrounding successful ($n = 9$) and unsuccessful ($n = 8$) breeding nests.[a]

| Dummy nests | Breeding nests<br>Unsuccessful | <br>Successful | Z | P |
|---|---|---|---|---|
| On territory | 7.1 ± 0.6 | 6.6 ± 1.2 | −0.68 | 0.25 |
| Within 5 m | 1.9 ± 0.7 | 1.1 ± 0.5 | −0.65 | 0.26 |
| Within 10 m | 3.9 ± 0.7 | 3.2 ± 0.6 | −0.85 | 0.19 |
| Within 15 m | 5.8 ± 0.5 | 4.7 ± 0.9 | −1.36 | 0.09 |

[a] Mann-Whitney *U*-test, all *P*s are one-tailed, $n$ = number of breeding nests.

Male Marsh Wrens built 2-12 nests on their territories ($\bar{x} = 6.4 \pm 0.6$). Males did not appear to need to build a minimum number of nests before attracting a mate. Some males that built only two nests had females nesting on their territories, whereas other males with many more dummy nests on their territories were unsuccessful in attracting females. There was no significant difference between the total number of dummy nests on territories where females nested (*active* territories) ($\bar{x} = 6.8 \pm 0.7$, $n = 17$) and those where no females nested (*inactive* territories) ($\bar{x} = 5.8 \pm 0.9$, $n = 13$, $t = -0.84$, $P = 0.21$).

The density of dummy nests in courting centers (*courting center density*) with more than two dummy nests of active territories ($\bar{x} = 0.19 \pm 0.05$ nests/m$^2$, $n = 16$) was not significantly different from the courting center density of inactive territories ($\bar{x} = 0.16 \pm 0.04$ nests/m$^2$, $n = 11$, $t = -0.44$, $P = 0.34$). Thus, female mate choice was apparently not influenced by the density of dummy nests on courting centers.

Female Marsh Wrens did not appear to select breeding nest locations based on the distribution of dummy nests within a territory. Within territories, I found no significant differences between the distance from breeding nests to their closest dummy nest ($\bar{x} = 4.2 \pm 0.5$ m, $n = 17$), and the distance between dummy nests and the next closest dummy nest ($\bar{x} = 3.7 \pm 0.3$ m, $n = 116$, $t = -0.68$, $P = 0.25$).

*Dummy nests did not reduce predation.*—All eight failures of breeding nests resulted from predation, with 75% attributable to mammals. I found no significant difference between the number of dummy nests within 15 m (following Leonard and Picman 1987b) of depredated and successful breeding nests (Table 1). There was no significant difference between the number of dummy nests within either 10 m or 5 m (arbitrarily chosen) of successful and unsuccessful breeding nests (Table 1). Nor did the total number of dummy nests within a territory affect breeding nest success (Table 1). Red-winged Blackbirds (*Agelaius phoeniceus*) also nested in the marsh, but they maintained a minimum distance of 15 m and were usually substantially farther from Marsh Wren courting centers. Because the only nests within courting center boundaries belonged to Marsh Wrens, there were no confounding effects caused by the presence of other species.

Breeding nest success was unaffected by the density of dummy nests in courting centers. The courting center density of territories that fledged young ($\bar{x} = 0.23 \pm 0.08$ nests/m$^2$, $n = 8$) was not significantly different from the courting center density of territories that were unsuccessful ($\bar{x} = 0.15 \pm 0.04$ nests/m$^2$, $n = 8$, $t = -0.98$, $P = 0.17$). Also, there was no significant difference in the distance from successful breeding nests to the closest dummy nest in the territory ($\bar{x} = 4.5 \pm 0.6$ m, $n = 9$) and depredated breeding nests to the closest dummy nest in the territory ($\bar{x} = 3.9 \pm 0.7$ m, $n = 8$, $t = -0.66$, $P = 0.26$).

Dummy nests built by male Marsh Wrens did not appear to attract females or reduce predation in this study area. Female Marsh Wrens did not preferentially nest on territories with more dummy nests or with high-density courting centers. Female nest-site selection did not differ from random with respect to the distance to dummy nests. Predators found breeding nests regardless of whether the nests used by females were close to dummy nests or surrounded by several dummy nests.

These results are in contrast with previous studies that investigated the possible adaptive significance of multiple nest building by male Marsh Wrens (Verner and Engelsen 1970, Tintle 1982, Leonard and Picman 1987b). Verner and Engelsen's (1970) and Tintle's (1982) studies supported the sexual selection hypothesis (i.e. there was a correlation between male pairing success and the number of nests a male built), whereas Leonard and Picman's (1987b) study partially supported the predator avoidance hypothesis (i.e. breeding nests surrounded by more dummy nests were more successful; females, however, did not preferentially settle on territories with more dummy nests). My results supported neither hypothesis.

Some differences between the results of these studies may be due to differences in habitat quality of the study sites, or behavioral differences between Marsh Wren populations. For example, eastern Marsh Wren subspecies have larger territories and are less likely to be polygynous than western Marsh Wrens (Kroodsma 1983). Despite the differences between the populations of Marsh Wrens, it seems that there should be a common explanation for why male Marsh Wrens build so many nests. The costs exacted on males by devoting time and energy to building multiple nests must be severe. Therefore, for this behavior to persist, some consistent benefits must be derived. Although my study was limited in scale and may not have reflected overall selective pressures, males that built the most nests were not compensated by attracting more females or by fledging more young. Other proposed benefits of multiple nests include the practice that males acquire (Hunter 1900), territory boundaries outlined by dummy nests (Allen 1923), or the burnoff of excess energy through nest building (Forbush 1929). These explanations have all been dismissed (see Welter 1935; Verner 1963, 1965). Verner (1965) hypothesized that dummy nests may be built as shelters for adults and newly fledged young. This does not explain why males should build many more nests than the number of young fledged and why females do not select males that build more shelters for their young. Nor does this hypothesis explain the variation among males in the number of nests built. None of the hypotheses proposed to date adequately explain the persistence of this phenomenon.

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# Facultative Helping by Pygmy Nuthatches

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In many cooperatively breeding birds, helping is a compulsory stage in the social development of individuals. Helpers enhance their chances of breeding in future years by increasing dominance status (Woolfenden and Fitzpatrick 1977), position in social queues (Woolfenden and Fitzpatrick 1978, Wiley and Rabenold 1984), or the probability of successful dispersal (Koenig 1981, Ligon and Ligon 1983, Hannon et al. 1985). Once individuals breed, reversal of social status is rare (but see Emlen 1981, Emlen and Wrege 1988, Curry 1988, P. B. Stacey pers. comm., for Acorn Woodpeckers, *Melanerpes formicivorous*). As an example, the White-fronted Bee-eater (*Merops bullockoides*) is known to revert to helping after breeding failure within a season or between seasons, a behavior termed redirected helping (Emlen 1981).

Recently, adaptive or functional explanations for helping have been challenged by the idea that helpers merely respond to a stimulus (i.e. nearby begging nestlings), which causes them to feed unrelated young (Jamieson and Craig 1987, Jamieson 1989, see Ligon and Stacey 1989 for a response). In this interpretation, helping behavior may be viewed as a consequence or byproduct of natal philopatry (see Stacey and Ligon 1987), which places young, nonbreeding birds in the proximity of begging nestlings. This hypothesis im-