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EFFECT OF EGG COVERING AND HABITAT ON NEST DESTRUCTION BY HOUSE WRENS[1]

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Abstract. Birds nesting near House Wrens (*Troglodytes aedon*) risk having their eggs, nestlings, and nests destroyed. Damage by wrens may be reduced in Black-capped Chickadees (*Parus atricapillus*), Tufted Titmice (*P. bicolor*), and other parids by concealing eggs under nest material during the laying period, and in sympatric cavity-nesting species by nesting in different habitats from wrens. To test if eggs were protected by covering, prelaying wrens were challenged for 1 day with a set of two boxes placed 1 m from their nest, one with two artificial eggs (miniature marshmallows) lightly covered under fur, the other with two artificial eggs in an open cup. Results varied with stage of nest-building; in 41 trials where both exposed eggs were removed, covered eggs remained in only 4 of 15 (27%) trials near early nests containing few sticks, but in 17 of 26 (65%) trials near more advanced nests. To assess effects of nest site, a box with a cup nest was placed in each of three habitats 10 or 20 m from 29 wren nests. After 1 day of habituation, two artificial eggs were placed in each nest and left exposed for 1 day. Boxes in woodland interiors were less likely than boxes in fields and along edges to be visited by wrens at least once over 2 days (66 vs. 97% visited) and were less likely to have eggs removed (10 vs. 83% removed). Competitors for nesting cavities also may escape attacks by wrens through differences in breeding period, active defense of territories or nests, or renesting.

Key words: House Wren, Troglodytes aedon, *egg destruction, nest destruction, egg covering, nest site selection.*

INTRODUCTION

House Wrens (*Troglodytes aedon*) of both sexes will destroy the contents and structure of nests of their own and other species (Sherman 1925, Belles-Isles and Picman 1986a). Wrens peck eggs or small nestlings, carry them from nests and discard them. They also may toss out nest linings. Such attacks may: (1) allow wrens to gain limiting cavities for nesting, renesting, second broods, and polygynous matings (Pribil and Picman 1991), (2) reduce competition for food in the local area (Creaser 1925), and (3) swamp search-strategy predators with empty nests (Finch 1990). In wrens, filial ovicide and infanticide are inhibited in mated males and in females that are laying or incubating eggs, or brooding nestlings (Belles-Isles and Picman 1986a, Kennedy and White 1996). Throughout the nesting period, however, wrens will attack nests at some distance from their own (Quinn and Holroyd 1989, Pribil and Picman 1991).

Nest destruction by wrens can be a major cause of breeding failure for co-occurring cavity-nesting species (Zeleny 1976, Smith 1991, Flaspohler 1996), and the extent to which wrens reduce the breeding density or range of other bird species has been a long-standing controversy (Sherman 1925, Kennedy and White 1996). Less attention has been given, however, to traits or behaviors in target species that allow them to escape, limit, or adjust to attacks by wrens. Attacks may be escaped by breeding before unmated wrens are present (Zeleny 1976) or after wrens are done breeding (Sherman 1925), by nesting in habitats less preferred by wrens (Belles-Isles and Picman 1986b, Finch 1990), or by nesting away from wren nests (Pribil and Picman 1991). Species at risk may respond directly to wrens or wren song with territorial displays or nest defense (Kendeigh 1941, Gorton 1977), or may limit losses by concealing eggs under nesting material (Haftorn and Slagsvold 1995). Finally, victims of attacks may renest successfully if they move (Sherman 1925) or breed in synchrony with the wren's inhibition period (Kennedy and White 1996). In this paper, we examine experimentally the effects of egg concealment and differences in nest habitat on risk of nest destruction by House Wrens.

During the egg-laying period, female Black-capped Chickadees (*Parus atricapillus*) and

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Tufted Titmice (*P. bicolor*) regularly cover their eggs with moss, fur and other soft material before leaving their nest cavity in the morning (Nickell 1956, Brackbill 1970). The female uncovers her eggs when she returns in the evening to roost. In nests of five *Parus* species in Norway, Haftorn and Slagsvold (1995) observed that females engaged in a series of pressing, pulling, and shuffling movements with their bill to cover their eggs over a 2–11 min period. They suggested that complex egg covering behaviors are a cost effective way for parids to reduce predation risk because predators are deterred by the combination of uncertainty over nest contents and moderate difficulty in inspecting small nest cavities. Under their model, egg covering would be ineffective when nest access is easy and unnecessary when nest access is difficult. Nest behaviors of North American nuthatches (*Sitta* spp.) are poorly known, but Eurasian Nuthatches (*Sitta europaea*) cover eggs during both laying and incubation periods (Pravosudov 1993, Haftorn and Slagsvold 1995). In this study, we asked whether burial of eggs during the laying period protects them from damage by wrens. Protection must be incomplete because wrens remain the major destroyer of eggs of North American parids (Smith 1991). Egg covering could not have evolved as a direct response to depredation by wrens because the behavior presumably is ancestral, occurring in all European parids (Haftorn and Slagsvold 1995). Nevertheless, egg tossing by wrens is potentially a selective factor that maintains covering behaviors, which vary among North American individuals and species.

We also asked, in an area occupied by wrens, how differences in nest habitat affect risk of nest damage by wrens. Several cavity-nesting species that are sympatric with House Wrens differ from wrens in their preferred nesting habitat (Willner et al. 1983, Pogue and Schnell 1994). House Wrens prefer to nest in open shrubby areas or along edges (Belles-Isles and Picman 1986b), whereas Eastern Bluebirds (*Sialia sialis*) and Tree Swallows (*Iridoprocne bicolor*) prefer more open fields (Zeleny 1976, Finch 1990), and chickadees and titmice prefer woodlands (Bent 1946). Promoters of bluebirds and other native cavity-nesting birds recommend placing nest boxes in specific habitats as one way to manage risk of attacks by wrens (Zeleny 1976). To test for effects of egg covering and habitat on nest destruction by House Wrens, we recorded how often wrens removed artificial eggs from experimental nest boxes placed near active wren nests.

METHODS

As a base for our experiments, nesting of House Wrens was monitored on an array of 65 nest boxes placed along the edges of young woodlands and tree rows bordering annually mowed, post-agricultural fields at the Whitehouse Nature Center of Albion College, Albion, Michigan (42°14′N, 84°4′W). Mature communities in the region are oak-hickory woodlands (Barnes and Wagner 1981). Along edges, dominant trees include black cherry (*Prunus serotina*), boxelder (*Acer negundo*), eastern cottonwood (*Populus deltoides*), shingle oak (*Quercus imbricaria*), red oak (*Q. rubra*), and American elm (*Ulmus americana*); tatarian honeysuckle (*Lonicera tatarica*) and gray dogwood (*Cornus racemosa*) shrubs were abundant. Fixed and experimental boxes (see below) were built identically of pine with interior floor dimensions of 10 × 10 cm and narrow entrance slots (4.5 cm wide × 2.5 cm high) to exclude swallows and bluebirds. Boxes were supported 1.3 m from the ground on ungreased metal poles to reduce disturbance by terrestrial vertebrate predators. To accommodate swallows and bluebirds, 31 larger boxes (floors 15 × 15 cm, entrance diameter 3.8 cm) were placed in fields 44–150 m from fixed boxes along edges.

ARTIFICIAL EGGS

Because experiments based on destruction of large numbers of songbird eggs raise ethical and practical concerns, we used artificial eggs. In preliminary work, we found that House Wrens treated miniature marshmallows like real eggs. Marshmallows (14 mm long × 13 mm in diameter) are edible white confections made from corn syrup, sugar, starch, and gelatin. They are about the size of wren eggs and are soft enough to be easily pierced or grabbed in the bill and carried from a nest by a wren. In two trials where a box with a dummy nest containing two marshmallows was placed 1 m from a box in which a wren was building a nest, the wren carried one marshmallow from the box just seconds after entering for the first time, then returned immediately and removed the second marshmallow. Speed, flight pattern, and vigorous displays of wrens were the same as those observed in similar previous experiments using eggs of House Sparrows *Passer domesticus* (Kennedy and White 1996).

Wrens were at least as likely to toss marshmallows as real eggs. In five separate trials, nest-building wrens were presented with boxes containing one marshmallow plus one infertile wren egg. Wrens first removed the marshmallow then the real egg in four cases, perhaps because white marshmallows are more visible than eggs in dark cavities. Both male and female wrens removed marshmallows. In one trial, a mated male twice entered a box but did not toss either the artificial or real egg, indicating that inhibitions against filial ovicide extended to marshmallows. To further test whether wrens treated marshmallows as eggs, a single marshmallow was added to each of eight incomplete wren clutches and left in the clutch for 24 hr or until removed by wrens. The marshmallow was removed in 5 of 8 trials, suggesting that wrens may perceive soft marshmallows as damaged eggs, which they will remove during laying. We saw no evidence of vertebrates attracted to marshmallows as food.

EGG COVERING EXPERIMENT

We tested the hypothesis that eggs covered with nest material, as done by Black-capped Chickadees and Tufted Titmice during the laying period, are less likely than uncovered eggs to be removed from nests by House Wrens. To determine whether risk of egg destruction might vary through the prelaying period, three stages of nest construction were defined for wren nests (Table 1). In the early stage, only a male may be present to toss eggs. In the middle stage, depending on when wrens pair, eggs may be tossed by the male or female. In the late stage when the female is lining the cup of sticks, mated males are not expected to toss eggs (Belles-Isles and Picman 1986a). Length of each nesting stage was calculated in 1995 for nests in which ≥ 1 egg was laid.

Each trial involved placing two boxes 1 m from a focal wren nest that was under construction. To verify the presence of a destructive wren, a control box was used that contained a dummy nest made of dried grass with two uncovered marshmallows. To test the protection hypothesis, an experimental box was used that contained a grass dummy nest plus an overlying cup of black dog fur simulating the soft lining of a parid nest. To model parid egg covering (Haftorn and Slagsvold 1995), we folded down the sides of the fur cup until two marshmallows in the center were concealed. As in real parid nests, the eggs could be discovered by simply teasing the lining aside with one finger. Coverage was deemed to provide protection from wrens if, after 24 hr, both uncovered marshmallows were gone from the control box but both covered marshmallows remained in the experimental box. Two marshmallows were used per box to force at least two wren visits to empty a box of artificial eggs and thereby solidify an inference of intentional egg tossing. Boxes were placed next to wren nests to maximize risk of egg destruction and thus challenge strongly the protection hypothesis. Trials were conducted 12 May–20 June 1995, to include both first and second broods; however, to limit pseudoreplication, only one trial was performed per wren nesting attempt.

TABLE 1. Nest building stages of House Wrens. In early nests, the male adds sticks until the box floor is completely covered. In the middle stage, the male fills the cavity and makes a cup of sticks. In the late stage ending with the first egg, the female adds a soft cup of fine material.

Stage	Description	Number of nests	Duration in days
Early	<floor covered	11	3.1
Middle	<complete male nest	14	3.1
Late	<first egg	19	3.4

HABITAT EXPERIMENT

We tested the hypothesis that risk of egg loss to wrens varies with the habitat of the target nest cavity. We expected that House Wrens would be reluctant to venture into open fields where Eastern Bluebirds and Tree Swallows nest (Zeleny 1976), but would be greater threats along edges and in adjacent woodland interiors where Black-capped Chickadees and Tufted Titmice nest. For each trial in our experiment, we selected a focal box located at a woodland and field edge and containing an active wren nest. On a radius of either 10 or 20 m from the wren nest, we placed three experimental boxes: an "open" box was placed to maximize exposure in the field, an "edge" box was placed on the field edge on the side most distant from the next nearest wren territory, and an "interior" box was placed in the

TABLE 2. Survival of sets of covered marshmallow "eggs" in experimental boxes in trials in which uncovered "eggs" were removed from control boxes.

Nesting stage	Number at risk	Number surviving	Percentage surviving
Early	15	4	27
Middle	18	11	61
Late	8	6	75

woodland perpendicular to the habitat edge. When the wooded habitat was narrow, the "interior" box was placed as deep as possible in the woods on the side away from the "edge" box. Radiuses of 10 and 20 m from the focal box were used to test for interactions of distance and habitat. Permanent boxes were separated by ~45 m, and at any one time never more than 40% of boxes contained wren eggs or nestlings.

A two-day protocol was employed for each trial. For the first 24 hr, we left empty dummy nests of dried grass and wood shavings in the experimental boxes. To tell if a wren had investigated a new box, we balanced a black wooden toothpick on wedges attached to the interior of the box on either side of the entrance slot. Pushing sticks through holes and leaving sticks protruding from holes are typical nest-building behaviors for wrens; videotaped trials verified that wrens did not hesitate to knock down a toothpick to enter a box. Following 1 day's habituation, two marshmallows were placed uncovered in each experimental box, and toothpicks were reset. Boxes were checked for wren entry and marshmallow removal after an additional 24 hr. Belles-Isles and Picman (1986a) interpreted their finding that mated male and egg-laying female wrens no longer attack eggs in nearby boxes as a generalization of an inhibition necessary to protect their own clutch. To test if a separation of 10–20 m between host and target nests relieved inhibitions against egg tossing, host nests in laying as well as building stages were used in trials. One trial per nesting attempt was conducted between 25 May–31 July 1996.

RESULTS

EGG COVERING EXPERIMENT

As expected from previous studies of egg tossing by prelaying House Wrens (Belles-Isles and Picman 1986a, Kennedy and White 1996), uncovered sets of marshmallows representing songbird eggs were removed readily from dummy nests placed beside wren boxes. In only 3 of 44 (7%) trials did uncovered marshmallows remain in control boxes after 24 hr. One of these 3 trials involved a completed wren nest that went on to have eggs, and was unexplained. The other two exceptions were attributable to an absent male (focal nest inactive for 2 weeks) and a female that had already started laying.

In the face of extreme risk, many artificial eggs were protected by burial under a nest lining of fur. In experimental boxes paired with controls from which uncovered marshmallows were removed, 21 of 41 (51%) sets of covered marshmallows survived exposure for 24 hr near an active wren nest. The proportion of surviving covered sets increased from about 1 in 4 placed near early stage wren nests to about 2 in 3 near middle and late stage nests (Table 2; test for effect of stage: $G_{\text{Yates}} = 4.35$, $P < 0.05$). Wrens did not tease apart nest lining in search for hidden eggs. Instead, marshmallow eggs apparently were discovered and removed as wrens cleaned out the lining and moved into experimental boxes (Table 3). Wrens in the early stage of nesting were most likely to move into experimental boxes because these boxes contained dummy nests that were larger than the wren's own nest.

Over two years, three pairs of Black-capped Chickadee and one pair of Tufted Titmice nested in boxes along edges within 42–49 m of active wren nests. Wrens destroyed only one brood of chickadee nestlings.

HABITAT EXPERIMENT

No significant difference was found in the frequency with which dummy nests were visited or marshmallow eggs were removed between 10 m and 20 m distances (Table 4). To have an 80% certainty of detecting distance effects of the magnitude observed, samples of 83–105 nests would be needed. It remains unclear how far along an edge a target nest must be from a host nest to escape damage by wrens. Attacks by

TABLE 3. Fate of dummy nests in experimental boxes in which covered marshmallow "eggs" were removed by wrens.

Nesting stage	n	Some nest lining gone	Most nest lining gone	Lining gone, sticks added
Early	11	1	4	6
Middle	7	0	4	3
Late	2	1	0	1

TABLE 4. Effects of distance and nesting stage on percentages of visitation and removal of marshmallow "eggs" per trial at boxes in three habitats near active nests of House Wrens.

Comparison	n	% boxes visited in all 3 habitats	% eggs removed from ≥2 boxes
Distance to wren nest			
10 m	22	73	82
20 m	7	43	57
G^{a}		0.95	0.64
Stage of wren nest			
building	20	75	85
egg-laying	9	44	56
G		1.36	1.48

[a] G_{Yates} value for a log-likelihood test; all $P > 0.10$.

wrens on clutches of other wrens occurred regularly at distances of ≥ 45 m from the nearest resident wren. Wrens destroyed at least 1 egg in 17 of 96 (18%) nesting attempts by wrens in permanent boxes over two years. Only 6 of 17 (35%) attacks resulted in total loss of a clutch.

No significant difference was found in frequency of visitation at dummy nests and in removal of marshmallow eggs between nest-building and egg-laying periods (Table 4). To have an 80% certainty of detecting nesting-stage effects of the magnitude observed, samples of 71–78 nests would be needed. Thus, wrens with a partial clutch of their own were not fully inhibited from tossing marshmallow eggs when dummy nests were placed ≥ 10 m from their own nest. However, inhibition of egg destruction appeared to protect some experimental nests. At nine boxes in nine separate trials, marshmallows remained in a box in which a fallen toothpick indicated that a wren had investigated the cavity. Marshmallows were removed from other boxes in seven of these nine trials. In two cases, the male wren was mated, but attacks would still have been expected from females. In four additional cases the female had begun laying. All trials were pooled to test for habitat effects.

Wrens were less likely to investigate and revisit experimental boxes in woodland interiors than boxes in open fields and along edges (Table 5). While 19 of 29 (66%) interior boxes were visited at least once over two days based on toothpicks being dislodged from entrance slots, 56 of 58 (97%) open plus edge boxes were visited ($G_{Yates} = 12.5$, $P < 0.001$). Only 3 of 14 (21%) interior boxes visited by wrens on day 1 were revisited on day 2 compared to 51 of 55 (93%) open plus edge boxes ($G_{Yates} = 25.4$, $P < 0.001$).

As expected, sets of marshmallow eggs that were added to experimental boxes that had stood empty for 1 day were frequently removed from boxes along woodland edges over 1 day's exposure. However, unexpectedly, eggs also were removed frequently from boxes in open fields and infrequently from boxes in interior woodlands (Table 5). No significant differences existed between open and edge boxes in frequency of visitation or of egg removal.

Wrens rarely attacked real nests in boxes placed permanently in fields 44–150 m from an edge. Of 18 Tree Swallow nests and 6 Eastern Bluebird nests in boxes in fields over two years, only 1 bluebird clutch was destroyed by wrens.

DISCUSSION

Our study suggests that chickadees, titmice, and other parids that cover their eggs with nest material during the day prior to incubation may reduce significantly the danger of egg destruction by House Wrens. Our finding that ~50% of buried eggs were uncovered and removed by wrens over one day is misleading because we purpose-

TABLE 5. Percentage of 29 trials in which a box placed in each habitat near a House Wren nest was visited, had marshmallow eggs remain undisturbed for 24 hr, or had sticks added as part of nest construction after "eggs" were removed.

Habitat	Visited day 1	Visited day 2	Eggs remain day 2	Sticks added day 2
Interior	48	28	90	0
Open	100	86	21	28
Edge	90	93	14	10
G^{a}	21.7	32.0	41.8	6.1
P	<0.001	<0.001	<0.001	<0.05

[a] G_{Yates} value for a log-likelihood test comparing interior vs. open plus edge boxes.

ly maximized risk by placing boxes with completed nests beside active wren nests. The sight or perhaps feel of an egg in a nest may be necessary to trigger egg-tossing. The nature of the egg appears irrelevant. Wrens attack with equal vigor conspecific eggs, heterospecific eggs of various sizes and colors in both cavity and cup nests (Belles-Isles and Picman 1986a), and small, white marshmallows. No evidence yet exits, however, that wrens dig for, can learn to dig for, or are capable of digging for covered eggs. Rather, hidden eggs appear safe unless discovered inadvertently as males remove nest linings to prepare clean stick cups for females (Kendeigh 1941). Thus, covered eggs may be safe from female wrens at all times and safe from male wrens that merely investigate a cavity because they are mated, or habituated to an existing nest, or because the cavity is in dense vegetation not preferred for nesting. Male wrens posed the greatest threat when they were initiating a nest. For successful nests, this early nesting stage lasted only ~3 days (Table 1). Male wrens that fail to attract a mate, however, can be a protracted risk to other birds' nests (Kennedy and White 1996). Danger posed by wrens before they begin nest building is unknown, although the period is brief for returning males in spring (Kendeigh 1941). The possibility that nesting activities near a target cavity, such as song, nest building, or feeding of mates or nestlings, will increase the risk of wren attack remains to be tested.

Results from both experiments were consistent with the hypothesis that wrens destroy nests to gain nesting cavities (Belles-Isles and Picman 1986a, Quinn and Holroyd 1989, Pribil and Picman 1991). Male wrens often took over new boxes within the allotted 1 or 2 days by adding sticks after removing artificial eggs and loose nest material. In the egg-covering experiment, nest usurpation was common early in nest building when dummy nests were larger than host nests (Table 3). Male wrens may have preferred experimental boxes because they would require less time or effort to fill with sticks (Kennedy and White 1992). In the habitat experiment, boxes in fields and along edges where artificial eggs were most at risk also were most likely to have sticks added; moreover, no sticks were added to woodland boxes (Table 5). This pattern corroborates the finding of Belles-Isles and Picman (1986b) that, given a choice, wrens prefer to nest in boxes in sparse versus dense vegetation. We did not expect that boxes placed 10–20 m into fields, which bluebirds and tree swallows use for nesting, would be readily attacked and usurped by wrens (Zeleny 1976). The annually mowed fields we used, however, appeared attractive to wrens when vegetation regrew; wrens even used "bluebird" and "swallow" boxes in field centers for second broods.

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