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OLD NESTS AS CUES FOR NEST-SITE SELECTION: AN EXPERIMENTAL TEST WITH RED-WINGED BLACKBIRDS[1]

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Abstract. This paper reports the results of an experimental test of the hypothesis that female Red-winged Blackbirds (*Agelaius phoeniceus*) should preferentially nest in areas containing old nests rather than in areas without them. The assumption that old nests can provide females with information about the nesting history of an area was supported by the finding that over 90% of redwing nests survived between two breeding seasons. Experiments to determine whether females actually respond to the relative density of old nests when selecting nest sites produced mixed results. In 1983, females built significantly more nests on seven experimental plots with old nests than on seven matched plots without old nests, but there were no significant differences between matched plots in 1984. Although these limited results do not support the old nest hypothesis, they do suggest that further investigation may be worthwhile.

Key words: *Old nests; habitat selection; Red-winged Blackbird; behavioral ecology.*

INTRODUCTION

When migratory female birds arrive on the breeding grounds at the beginning of the nesting season, little information may be available to them for judging the quality of nesting habitat. The food supply upon which breeding success will depend may not be present or may not be representative of what will be available later in the season. The foliage that serves to conceal nests from predators or to support nests may not be fully developed, and potential predators may not be present at densities or in locations typical of the nesting period. Because information related directly to these critical factors is often limited when females are prospecting for nest sites, females may rely on indirect cues in choosing areas for breeding and specific sites for nesting (Lenington 1980, Cody 1985).

Among cues that female birds use in selecting nest sites are the presence of already settled individuals, the configuration and quality of vegetation, signs of future food availability (e.g., insect egg cases), and, when the females are returning to an area in which they have nested before, memories from previous breeding attempts (Lenington 1980). In selecting breeding sites, females should use the set of available cues that most reliably predicts future conditions influencing breeding success. One such potential cue, the presence of nests from the previous nesting season, is the subject of this paper.

Among small passerine birds, nests are rarely used more than once, and nests are not designed for great longevity. However, because many nests do survive from one breeding season to the next, old nests potentially provide prospecting females with cues related to past breeding activity. The presence of old nests in marshes in which Red-winged Blackbirds (*Agelaius phoeniceus*) breed suggested that female redwings might use information provided by old nests in selecting nest sites. In a pilot experiment conducted over a 3-week period in 1982, female redwings were found to nest preferentially in plots to which old nests had been added.

Based on these results, more extensive and better-controlled experiments were conducted to test the hypothesis that female redwings preferentially nested in areas containing old nests, rather than in areas without them. In this paper, we first present evidence demonstrating that the survival of redwing nests between breeding seasons is high

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enough that the density of old nests may serve as an acceptable index of nesting density in the previous breeding season. We then show that human observers can make reasonably accurate guesses concerning the success of breeding attempts at individual nests in the previous nesting season by examining old nests. Finally, results are presented from experiments in which the density of old nests was manipulated on nesting territories.

The Red-winged Blackbird is an abundant breeding bird in marshes over much of North America. In the Pacific Northwest, redwings nest primarily in marshes dominated by emergent cattails (*Typha latifolia*) or bulrushes (*Scirpus* spp.). In selecting nest sites, female redwings are influenced by water depth and by the density, geometry, and quality of emergent vegetation (Lenington 1980, Orians 1980). Female redwings may also select territories on the basis of the characteristics of the male owner, but evidence indicates that characteristics of a territory are far more important to females (Searcy 1977, Searcy and Yasukawa 1983).

STUDY AREAS AND METHODS

Study marshes were located in lakes on the Columbia National Wildlife Refuge, in central Washington. The general features of the lakes and the ecology of redwings in the area have been described by Orians (1980). Redwings in this area typically begin nesting in late March or early April. Although some egg laying may continue into late June, most nesting activity is completed by mid-June. Because all males and most of the females were color-banded during this study, breeding histories were available for many of the individuals that settled in the experimental study areas.

Experiments were conducted during 1983 and 1984 on strip cattail marshes that surround McMannaman Lake and Hampton Slough (see Beletsky and Orians 1987 for a map). The marshes were only one territory in width from the shoreline to open water. On 18 March 1983, eight strip-marsh plots, each 40 m long, were established in a continuous series along the south and east sides of McMannaman Lake. Adjacent plots were reasonably well matched with respect to the area and geometry of cattail marsh within them. The same procedure was followed in establishing three pairs of plots on Hampton Slough on 19 March 1983. All experimental plots were searched, and all old nests were removed. The number of old nests found in each plot was recorded. To avoid interference by dominant male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), experimental plots were located in sections of marshes in which yellowheads rarely nested. Over 300 redwing nests that had been constructed in 1982 were collected from nearby marshes, stored over winter, and used to add to experimental plots.

Each plot received either 24 old nests or no old nests. A coin flip was used to designate the experimental treatment of the northwesternmost plot on each lake, and treatments were alternated between plots along the shorelines. Old nests were placed throughout each designated experimental plot. Nests were placed in small cattail clumps between 0.6–1.3 m above the water. These are typical sites for redwings in the study area. Nests were fastened with nails and yellow tape to wooden dowels, and the dowels were attached to dead cattails with yellow tape. This method provided good support for the nests. Yellow was selected because it was inconspicuous against the light brown background of dead cattails. All nests were placed in experimental plots before females settled on territories. The plots were searched at intervals of 3–6 days throughout the breeding season until about 15 June, by which time nearly all redwing nests had been initiated. All new nests were marked and numbered, and their status was checked every 3 days.

The same experimental procedure was followed in 1984, with two exceptions. First, old nests used in the 1984 experiments were collected from the experimental plots and nearby marshes in late February, approximately 3 weeks before the time the experiments were started (18–19 March). Second, the assignment of experimental status was reversed, so that plots receiving nests in 1983 received no nests in 1984 and vice versa. Although nests used in 1984 had been exposed to winter weather, the range of condition among those nests was comparable to that among nests used in 1983. In addition, in both years we used only nests in relatively good condition. Therefore, significant differences did not exist between nests used in the two years.

The natural survival rate of nests between breeding seasons was estimated in February 1984 by recording the presence or absence of 142 nests that had been constructed in 1983. To evaluate whether female redwings might be able to use the condition of an old nest as an indicator of the breeding success of the female using that nest the previous year, 109 nests were rated as either successful (fledged) or unsuccessful by two observers. Neither of the observers was familiar with the details of breeding success in those marshes in 1983.

RESULTS

SURVIVAL RATE OF OLD NESTS

If old nests are to serve as reliable indicators of habitat quality, a large enough proportion of them must survive to provide an adequate index of nesting density in the previous year. Of 142 nests built on and near experimental plots in 1983, 131 (92%) were still present in February 1984. This result is consistent with our observations that, in the absence of major blow-downs of cattails, most redwing nests survive over winter in these marshes. Because nests rarely survive over a second winter, the density of old nests present at the beginning of a breeding season usually is a reliable index of the density of nesting in the previous year.

CONDITION OF OLD NESTS

Although old nests may provide an index of breeding density, this is not necessarily an index of breeding success in the previous year. For example, a high density of nests might result from a high rate of nest predation combined with a high rate of renesting by females. Some females build up to five unsuccessful nests in a single breeding season (Picman 1981, Orians and Beletsky 1989). To serve as a reliable predictor of habitat quality, the appearance of old nests must provide information regarding their fate.

The characteristics of old nests do reflect their history. For example, nests from which eggs were taken by snakes or birds, the major nest predators in our area, are often intact. In contrast, nests from which young fledged are often flattened and covered with droppings from larger nestlings. These qualitative observations are supported by the results of our systematic classification of old nests collected in 1984.

Observers classified as successful 12 (63%) of 19 nests that actually either fledged young or reached the stage of having large nestlings before being robbed by predators. (Nests that were too deteriorated to classify [$n = 5$] and in which mice had constructed nests [$n = 4$] were excluded from the analysis.) Observers classified as unsuccessful 66 (81%) of 81 completed nests that actually did not receive eggs or that lost eggs or small nestlings to predators. The success of observers in guessing the fate of nests was significantly better than that predicted by chance alone ($\chi^2 = 13.377$, df = 1, $P < 0.001$). Observers also correctly classified as incomplete 11 (73%) of 15 nests that were started but never completed. If female redwings are at least as good as biologists at judging the fate of old nests by their appearances, then they could derive information about nesting success in the previous year by examining old nests.

TABLE 1. Number of Red-winged Blackbird nests built on experimental plots with and without old nests on Hampton Slough and McMannaman Lake, Columbia National Wildlife Refuge, during 1983 and 1984.[a]

	Total nests built on plots[b]			
	1983		1984	
Plot pair	Without	With	Without	With
McMannaman Lake				
M1	3	6	6	6
M2	6	15	7	3
M3	12	9	11	15
M4	1	6	8	5
All	22	36	32	29
Hampton Slough				
H1	11	15	7	8
H2	5	12	10	4
H3	5	5	10	6
All	21	32	27	18
Total nests built	43	68	59	47

[a] All old nests were removed from all plots prior to experiments. Duration of experiments in both years was 18 March–15 June.
[b] Only nests that received eggs were counted.

NEST MANIPULATION EXPERIMENTS

A significant tendency for females to nest preferentially on plots with old nests was evident in the 1983 experiment (Table 1, paired $t = 3.57$, df = 6, $P = 0.03$). However, in 1984, when experimental treatments were reversed, females showed no preference for plots with old nests (paired $t = -1.30$, df = 6, $P = 0.24$). An analysis of the combined data from both years revealed no significant preference for plots with old nests (paired $t = 0.76$, df = 13, $P = 0.29$). The total number of nests built on all experimental plots was 111 in 1983 and 106 in 1984.

Prior to the start of the 1983 experiment, 53 old nests were removed from the plots to which old nests were to be added, and 46 old nests were removed from the plots that were to receive no old nests. Thus, both experimental and control plots attracted similar numbers of females in 1982, suggesting differences in habitat quality did not bias our results.

DISCUSSION AND CONCLUSIONS

This study addressed two questions. First, can old nests serve as reliable cues to the quality of nesting habitat for female Red-winged Blackbirds? Second, do female Red-winged Blackbirds actually use old nests as cues when choosing areas for nesting? More precisely, do they preferentially nest in areas containing old nests?

Nests of redwings on experimental plots survived over the winter of 1983–1984 at a high rate, and the ability of observers to guess whether old nests had been successful or unsuccessful was significantly better than random. Thus, both the density of old nests and their condition could provide prospecting females with cues relating to habitat quality. However, these cues should be used by females for habitat selection only if nesting density and breeding success in one year in a given area predict breeding success the following year. Both nesting density and breeding success were positively correlated between years on the different marshes in our study area over an 8-year period (Beletsky and Orians 1987). Therefore, old nests do provide reliable clues about current breeding conditions.

If females avoid areas where nesting success was poor the previous year, our experimental design would have been biased against the old nest hypothesis. Because the rate of nest failure is typically 60–70% in our study area, most of the nests we placed on experimental plots were probably unsuccessful ones. Nonetheless, most females return to the same marsh to nest in subsequent years in spite of the low average nesting success rate. Therefore, the presence of unsuccessful old nests does not deter females from settling in a marsh although it might influence behavior on a scale of a few meters.

Female redwings nested preferentially on experimental plots with old nests during the 1983 experiment, but not during the 1984 experiment. The combined data from both years revealed no overall tendency for females to settle on plots with old nests. The degree to which female redwings use old nests as cues for settling, then, is at best limited.

The positive results obtained in 1983 are probably not due to differences in the inherent quality of plots receiving the two types of experimental treatment. The pairs of plots were well matched with respect to the amount and type of habitat included. The pairs of plots receiving each type of experimental treatment were adjacent and arranged in two continuous series, making a systematic bias in habitat quality unlikely. Furthermore, similar numbers of females nested in the two types of plot in 1982, indicating that females perceived them to be of similar quality the previous year.

The positive 1983 results could represent a real preference by females for settling near old nests. If so, nest-site fidelity, which is typical of female redwings (Picman 1981, Orians and Beletsky 1989), could explain the negative results in 1984. However, this explanation is unlikely because, of the 12 color-banded females present on experimental plots in 1983 that returned to the refuge in 1984, none nested in the same plot in 1984.

Nonetheless, most female redwings do return to the same general breeding area in subsequent years. They may use old nests as cues for habitat selection but at a scale different than the size of our experimental plots. For example, females could have used old nests as an indicator of the overall quality of a breeding area, while choosing specific nesting sites within a marsh using factors other than the local density of nests. Our experiment could not have detected the influence of old nests on that scale (Orians and Wittenberger, in press).

Temporal patterns in the value of particular cues to habitat quality may also affect the results of our experiments. The value of old nests as cues for habitat selection should decrease as the breeding season progresses and more direct information on current habitat quality becomes available. In particular, the number of females incubating and feeding nestlings in a marsh is a better indicator of habitat quality later that season than is the density of old nests. To determine whether there might be a temporal trend in the tendency of females to settle near old nests, we analyzed the numbers of new nests started on plots with and without old nests by 2-week periods for the 1983 and 1984 experiments. There were no significant differences among 2-week periods for either year.

To test whether late-arriving females preferentially settled near active nests, an analysis of settling patterns of females in 1983 was performed by plotting both new nest starts and active nests at 3-day intervals on maps of Hampton Slough and McMannaman Lake. Inspection of the maps did not reveal any tendency for females either to settle near or to avoid active nests. Even when the presence of only nests that had nestlings was considered, no trend was apparent. This analysis indicates that late-arriving females in this study did not use the activity of nesting females as a cue for selection of nest sites within marshes.

Although our results indicate that old nests are of little or no importance as habitat-selection cues for female redwings, old nests may be useful in other species. Old nests could be important among species for which the survival rate of old nests is high, correlations between nesting density and nesting success are strong between years, nesting density correlates strongly with habitat quality, few other cues for habitat quality are available when females must select nest sites, site fidelity is low and prior knowledge of breeding areas is limited, or appropriate nesting sites are limited and widely spaced.

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