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BROWN THRASHER NEST REUSE: A TIME SAVING RESOURCE, PROTECTION FROM SEARCH-STRATEGY PREDATORS, OR CUES FOR NEST-SITE SELECTION?[1]

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Abstract. We examined the potential functions of old nests in a population of Brown Thrashers (Toxostoma rufum) nesting on the Konza Prairie Research Natural Area in northeastern Kansas. We determined whether thrashers reuse nests constructed in previous years, and tested predictions of the hypothesis that old nests function to reduce the risk of nest predation by saturating the cues used by search-strategy predators. We also manipulated old-nest densities to test the hypothesis that old nests are used as indirect cues for nest-site selection. Thrashers were found to reuse nests, albeit at low rates (4% of nests monitored). We found no significant relationships between the density of old nests and the success of active nests, and experimentally removing nests did not influence nest-site selection. These results suggest that old nests may only benefit thrashers in this population as a resource to reduce the time spent in nest construction.

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Key words: Brown Thrasher, nest-reuse, nest-site selection, old nests, Toxostoma rufum.

Considerable variation exists in the longevity of open cup nests built by passerines. Some nests deteriorate during, and shortly after, a nesting attempt (Skutch 1976, Briskie and Sealy 1988), whereas others may last for several years (Watts 1987). The accumulation of old nests on the territories of breeding birds has led to the supposition that they may provide an adaptive function. Three hypotheses proposed for the function of old nests include: (1) old nests may be reused and thus, provide a savings in time and energy to parents, (2) the accumulation of old nests may provide protection from search-strategy predators (Watts 1987), and (3) old nests may function as an indirect cue for nest-site selection (Erckmann et al. 1990). These hypotheses are not mutually exclusive and may act in concert, depending on the species and the local environment in which it breeds. Despite the potential adaptive function of old nests, these hypotheses have been largely untested. The reuse of nests constructed in previous years has been well documented for cavity breeders (Nilsson 1984, Brawn and Balda 1988), and species that place their nests on ledges (Skutch 1976). However, few open nesting passerines have been found to reuse old nests (Clark and Mason 1985) and only recently has

the reuse of old nests been confirmed for Western Wood-pewees (*Contopus sordiduls*; Curson et al. 1996), Least Flycatchers (*Empidonax minimus*; Briskie and Sealy 1988), Western Kingbirds *(Tyrannus verticalis*; Bergin 1997), and Cedar Waxwings (*Bombycilla cedrorum*; Mountjoy and Robertson 1988).

We tested predictions of these hypotheses in a prairie population of Brown Thrashers (*Toxostoma rufum*). We felt the Brown Thrasher was an ideal species to use for several reasons: (1) thrashers build large sturdy nests that can last for many years (J. F. Cavitt, pers. observ.), (2) because old nests are abundant and nest predation is high in this population, old nests may serve a protective function, and (3) because woody vegetation is sparse on the prairie, this population may be limited in the number of suitable nesting sites. Thus, we documented the extent and frequency of nest reuse in this population and tested predictions of the "predator protection hypothesis" and the "nest-site limitation hypothesis."

We predicted that if the presence of old nests can saturate the search cues of predators, then a positive relationship should exist between the proportion of nests that are old and the success of active nests on each study plot. If old thrasher-nests function as a cue for nest-site selection, then thrashers should preferentially select sites with the greatest density of old nests. We further predicted that the experimental removal of old nests should result in thrashers avoiding or delaying nest initiation on removal sites relative to unmanipulated control sites.

METHODS

STUDY AREA AND SPECIES

This study was conducted from 1995–1996 on the Konza Prairie Research Natural Area located in Riley and Geary Counties of Kansas (39°05'N, 97°35'W). Konza lies within the Flint Hills physiographic province and is a 35 km² ecological preserve owned by the Nature Conservancy and managed by the Division of Biology of Kansas State University. The Flint Hills region of Kansas is characterized by steep-sided hills exposing alternating limestone-shale layers and is dominated by warm season prairie grasses. Scattered patches of shrubs and trees can be found throughout the prairie but tend to be concentrated along limestone outcrops and along streams that drain upland sites (Zimmerman 1993). The low density of woody vegetation found throughout this tallgrass prairie site may limit thrashers in appropriate nesting sites.

In the Flint Hills of Kansas, Brown Thrashers are migratory, arriving in early April, and are single brooded, initiating nests in late April and early May (Zimmerman 1993, Cavitt, in press b). Nests are constructed of twigs and grasses (Erwin 1935, Partin 1977) and on Konza are placed primarily within patches of rough-leaved dogwood (*Cornus drummondii*) and plum (*Prunus* sp.), in small trees (e.g., *Ulmus americana*), or in shrubs such as aromatic sumac (*Rhus aromatica*). Nest construction is shared equally by both parents and can last from 3 days to over a week (Erwin 1935). Brown Thrashers are socially monogamous with both parents participating in incubation and brooding (Erwin 1935, Partin 1977).

GENERAL PROCEDURES

Seven study plots (20–100 ha) on Konza were utilized for this study. Active nests on each plot were located by systematic searches of potential nest sites, observing the behavior of adults, and by checking old nests from previous years. Once discovered, nest locations were plotted on an aerial photograph of the study site. Nest searching was intense on these sites and thus, all nests initiated were eventually located. The status of extant nests (presence of eggs, nestlings, parents) was checked by visitations every 3–4 days. Nests were defined as successful if at least one nestling survived to nest-leaving. A failed nest was classified as depredated if all eggs or nestlings disappeared prior to the expected date of nest-leaving and there was no basis for weather induced mortality.

Prior to the arrival of thrashers in late March and early April of 1996, study plots were systematically searched for old thrasher-nests. Because foliage was virtually absent on nesting substrates when searches were conducted, all old nests were easily located. Each old nest was individually marked with a small plastic tag (~ 6 × 2 cm) attached to the base of the nest and classified according to condition. The condition of each nest was classified as "good," if the nest lining was intact, the nest bowl was sturdy, and there were no gaps or holes present; nests were classified as "fair," if the nest lining was missing but the nest bowl was in "good" condition; a classification of "poor" was assigned if the nest lining was missing and the nest bowl had obvious gaps or holes.

NEST REMOVAL EXPERIMENT

We conducted a nest removal experiment to determine whether old nests are used by Brown Thrashers as a cue for nest-site selection. Prior to the arrival of thrashers in 1996, upland drainages (draws), not used for intensive thrasher monitoring as described above, were systematically searched for old nests. Twenty draws of similar length were selected that contained one or two old thrasher-nests. Each draw was randomly assigned as either a removal (*n* = 9) or control treatment (*n* = 11). We removed all nests discovered in draws allocated to the removal treatment and individually tagged and numbered nests located in control draws. After the arrival of thrashers, each draw was systematically searched for the presence of new nests once every week. Draws were utilized as the experimental unit rather than whole study plots because they are discrete units that contain only a single thrasher territory and are amenable to a replicated design.

STATISTICAL ANALYSES

Programs contained on SAS-PC (SAS 1996) were used for most statistical analyses. Assumptions of normality and homogeneous variances were tested for each analysis. Pearson product moment correlations were used to determine whether associations exist between variables. Daily survival rates and nest success estimates were determined according to the Mayfield (1961, 1975) method as modified by Johnson (1979) and Hensler and Nichols (1981). Correlations between nest density and the survival of nests were made by using both the Mayfield estimate of nest success as well as

the daily survival rate of nests during the incubation period. The daily survival rate during the incubation period was used in correlation analyses because one study plot did not produce any nests surviving past the incubation period. Log-likelihood tests (G_{adj} value reported) with William's corrections for sample size (Sokal and Rohlf 1981) were used for tests of independence. Alpha levels of 0.05 were considered significant. Values reported are means $\pm$ SE.

RESULTS

A total of 104 old nests were marked on seven plots during the early spring of 1996. However, the density of old nests among study plots was variable and ranged from 0.06–0.96 nests ha^{-1}. The majority of old nests were structurally sound with only the nest lining missing or torn. Approximately 82% of nests ($n = 85$) were classified as in good or fair condition.

NEST REUSE

During the 1995 breeding season, we suspected that 3% of 90 nests monitored were reused by Brown Thrasher parents and an additional nest built in 1995 was reused within the same breeding season. Of the old nests marked in the early spring of 1996, four were used during the breeding season. Thus, 4% of 94 nests monitored for this study in 1996 were initiated in old nests, but no within-season nest reuse was observed. Three of the four old nests reused in 1996 successfully fledged young the previous year, whereas the fourth was depredated during incubation. Clutches in old nests were initiated earlier in the breeding season than clutches laid in new nests ($t_{137} = 2.1$, $P = 0.03$; Julian date of clutch initiation for reused nests = 140.0 $\pm$ 7.6, new nests = 157.4 $\pm$ 1.8). Three of the pairs using old nests had nest contents consumed by predators and only one pair successfully fledged nestlings.

ROLE OF OLD NESTS IN PREDATOR PROTECTION

We found no significant relationship between the density of old nests and the success of nests initiated in 1996 ($P > 0.6$). Furthermore, the total density of nests (old + new nests) on each plot was not significantly correlated with nesting success or the daily survival rate during the incubation period (both tests $P > 0.4$).

ROLE OF OLD NESTS IN NEST-SITE SELECTION

We found no significant relationship between plot size and the number of old nests ($P > 0.6$). Sites with the greatest number of old nests had more new nests initiated during the 1996 breeding season (Fig. 1). Yet, first thrasher-nests were not initiated earlier on plots with the highest density of old nests nor was the average date of nest initiation significantly related to the density of old nests ($P > 0.4$).

The results of the nest removal experiment did not support the nest-site selection hypothesis. The proportion of control draws containing at least one nest initiated in 1996 was greater than removal draws (control = 0.64, removal = 0.33), but the difference was not significant ($G_{adj} = 1.7$, $P > 0.6$). There was no significant difference between treatments in the Julian date of clutch initiation ($t_{10} = 0.09$, $P = 0.94$) or the mean number of nests per draw ($t_{18} = 1.2$, $P = 0.24$).
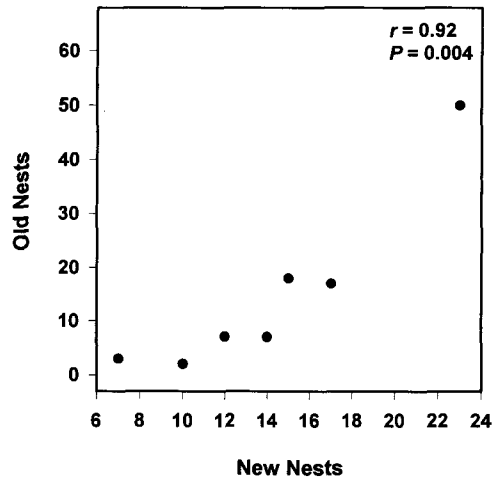

FIGURE 1. Relationship between the number of Brown Thrasher old nests present per plot and the number of new nests subsequently built.

DISCUSSION

Approximately 20% of North American passerine species reuse old nests constructed in previous years, but nests are rarely reused by open nesting passerines (Clark and Mason 1985). The reuse of old nests potentially saves thrashers between 3–8 days in nest construction (Erwin 1935). Because of seasonal declines in the condition of nestlings at nest leaving (Cavitt, in press b), this time savings may have important consequences for the reproductive success of parents.

Despite this potential benefit, the observed frequency of reuse was low (4%). Thus, the costs of nest reuse may limit the occurrence of this phenomena. Costs in increased ectoparasite loads for birds that reuse nests have been documented for cavity nesters (Rendell and Verbeek 1996), and mites occur within thrasher nests and on nestlings (J. F. Cavitt, pers. observ.). Costs in the structural integrity of old nests may not be important for this population. During three years of intense nest monitoring, we recorded only seven incidences (2% of nests monitored) of nests blown or knocked loose from the nest substrate. Furthermore, none of the nests known or suspected to be reused failed because of compromises to the structural integrity of the nest.

Erckmann et al. (1990) suggested that birds may be able to use the condition of old nests to determine the success of breeding attempts in the previous season. They reasoned that Red-winged Blackbird (*Agelaius phoeniceus*) nests depredated during the egg stage are often intact, whereas nests that fledged offspring are often flattened and covered with the droppings of larger nestlings. Thus, females prospecting for nest sites may use these cues in deciding where to build their nest. For species such as the Brown Thrasher which construct bulky nests made of twigs, the nest is not typically flattened by the weight of nestlings and only rarely is fecal material found after nestlings have fledged. Thus, it is not likely that thrashers can use characteristics of old nests as an index of its breeding history.

Although nest predation in this population is one of the highest reported for Brown Thrashers (Cavitt 1998), the presence of old nests does not appear to provide protection from predators. Because snakes are major nest predators (Cavitt, in press a), the lack of any significant effect of old nests on nest success is perhaps not surprising. Snakes have long been assumed to utilize parental activity to locate nests rather than developing a search image (Skutch 1949, 1985). Old nests may provide protection in other populations or species where search-strategy predators are common (Martin 1987, 1993, Watts 1987).

Sites with the greatest number of old nests had the greatest number of new nests constructed. However, thrasher parents did not initiate nests sooner on plots with the highest old-nest densities, nor did experimental removal of old nests influence nest-site selection. Thus, the presence of old nests does not likely influence nest-site selection in Brown Thrashers. The high rate of nest predation combined with frequent renesting results in a high density of old nests on Konza. Because it is unlikely that thrashers can determine past breeding history from the condition of old nests, other factors, such as nest concealment, may be more important in determining nest-site selection (Martin and Roper 1988). Thus, use of old nests as cues for the placement of new nests is likely a poor strategy for this population.

Although old nests are a conspicuous portion of the thrasher's environment, these data suggest they do not function to reduce predation risk or as cues for nest-site selection. Rather, this population of thrashers may reuse nests as a time saving resource.

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