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Within-season Nest-site Fidelity in Eastern Bluebirds: Disentangling Effects of Nest Success and Parasite Avoidance

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ABSTRACT.—We manipulated nestbox choices in Eastern Bluebirds (*Sialia sialis*) to assess (1) whether the presence of a previously used (and presumably parasite-ridden) nest cavity increases or decreases the likelihood of within-season nestbox reuse and (2) whether birds prefer previously successful cavities. Initially, birds were presented with two clean identical nestboxes erected 1 m apart. After the first nesting, we removed nest material from half of the successful box pairs and recorded subsequent nesting choices. Given a choice between a used and an unused box, bluebirds chose the unused but parasite-free cavity significantly more often. Presented with a cleaned successful box and an identical unused one, bluebirds opted to reuse the former significantly more often. Those results suggest that (1) bluebirds recognize a cost of within-season nest reuse and are willing to switch nest sites to minimize parasitism, (2) bluebirds prefer successful cavities, but only if they are clean, and (3) in our population, in which cost of nest switching was minimized, the aversion to parasites was stronger than the preference for successful cavities.

In recent decades, a contentious discussion has taken place in the literature as a result of two opposing assumptions about nest-site reuse—that birds either prefer or avoid used cavities. Birds may prefer to reuse successful cavities either because construction of a new nest may constitute a significant time and energy cost (Conrad and Robertson 1993, Gauthier and Thomas 1993), because successful cavities are more valuable than untested sites (Thompson and Neill 1991), or simply because suitable nest cavities are rare. Indeed, a variety of avian species have been shown to exhibit a preference for soiled nests (Jackson and Tate 1974, Davis et al. 1994, Mappes et al. 1994) or at least lack of aversion to them (Thompson and Neill 1991, Johnson 1996, Blem et al. 1999).

Conversely, birds may avoid used nests due to the ectoparasites they contain. Both observational and experimental research has demonstrated that nest ectoparasites can reduce reproductive success (Loye and Carroll 1991, deLope and Møller 1993, Richner et al. 1993, Christe et al. 1996). Not surprisingly, some birds have been shown sensitive to costs associated with parasites. Some species have been shown to discriminate between high and low infestation levels in used nests and choose accordingly (Brown and Brown 1986, Barclay 1988, Oppliger et al. 1994, Rendell and Verbeek 1996). These results suggest that multibrooded secondary cavity nesters should take steps to minimize parasitism costs associated with being multibrooded.

To assess relative importance of nest success versus presence of soiled nests in the nest-site reuse decisions of Eastern Bluebirds (*Sialia sialis*), we performed a controlled experiment addressing those two conflicting variables simultaneously.

Methods.—The Eastern Bluebird is a common, socially monogamous, secondary cavity nester (Gowaty and Plissner 1998). In North Carolina, bluebirds regularly produces two, and sometimes three broods of young per season (M. Stanback unpubl. data), often in the same cavity (Gowaty and Plissner 1997). Ectoparasites, including fleas, lice, mites, and blowfly larvae, are known to reside in the nests of Eastern Bluebirds (Burtt et al. 1991). Unlike some other species of cavity nesters, such as House Wren (*Troglodytes aedon*) (Johnson 1996), bluebirds do not remove old nest material from cavities, but simply build over an existing nest.

One hundred pairs of identical bluebird nestboxes were erected in suitable habitat near Davidson, Mecklenburg County, North Carolina. The box pairs consisted of two Schwegler "woodcrete" boxes. "Woodcrete" is a mixture of sawdust and cement. All box pairs were pole-mounted 1 m apart, 1.75 m above ground level, and both boxes within each pair faced the same direction. Between breeding seasons every box was cleaned. Consequently, at the beginning of each breeding season, bluebird pairs at a particular location were choosing between two identical clean boxes for their first nesting. We considered a

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nestbox chosen when at least one egg was laid in it and a nesting successful if it fledged at least one chick. We omitted renests following failures from our analyses because bluebirds and other species are more likely to change breeding sites if the previous attempt fails (Jackson et al. 1989, Gowaty and Plissner 1997).

After the first nesting, we randomly assigned box pairs containing a successful box to one of two treatments. For half of those box pairs, we removed all old nest material (and presumably most of the active parasites) from the used box within one week of the first brood's fledging. Those experimental boxes are hereafter referred to as *cleaned.* The clean unused boxes in those experimental pairs are hereafter referred to as *unused.* For control box pairs, the boxes were visited, but the old nests were not removed. These boxes are hereafter referred to as *soiled* and the alternative boxes, *unused.* Subsequent nesting choices in both experimental and control pairs were then recorded. Differences between the treatments were identified using a G-test with Williams' correction.

Results.—When adults were forced to chose between a soiled but successful nestbox and an unused nest site of equal quality, 71% of bluebirds chose to move to the unused box (of 45 bluebird pairs, 32 pairs switched to the unused box; 13 reused the soiled nest). In the experimental treatment, we investigated whether bluebirds were avoiding the soiled nest or the used box. When presented with a choice between an unused box or a cleaned used box, 75% of the pairs renested in the latter (32 bluebird pairs; 24 pairs chose the cleaned used box; 8 pairs chose the unused box). There was a highly significant effect of nest removal on renesting decisions ($G_{adj} = 15.0$, $P < 0.001$).

Discussion.—Under natural conditions, renesting bluebirds have limited options. Alternate cavities may be scarce, distant, defended, suboptimal, of unknown quality, or themselves soiled. If ectoparasitism costs are typically less than the costs of within-season nest-site changes, one might expect nest-site-limited species to reuse successful nest sites, regardless of their cleanliness. Such a rule of thumb is not apparent in our population.

If costs of parasitism typically outweigh costs of nest-site switching, one might expect bluebirds to avoid recently used cavities, regardless of their cleanliness. Again, we find no evidence of such a rule of thumb. Instead, bluebirds made situation-dependent assessments. Given a choice between a soiled and an unused box, bluebirds were very willing to switch to an "untested", but parasite-free cavity located in the immediate vicinity. Presented with a cleaned successful box and an identical unused one, bluebirds opted to reuse the former. Faced with a novel situation, specifically a clean successful cavity, bluebirds responded apparently optimally.

However, the generality of our results may be limited to within-season nest-site reuse in secondary cavity nesters. Despite recent interest in effects of parasites, little effort has been made in the literature to distinguish within- versus between-season nest-site reuse. In fact, with the exception of Gowaty and Plissner (1997), most published studies of nest-site reuse focus on between-season patterns. With respect to ectoparasites, those two types of nest reuse are very different. First, within a season, there is a much greater probability that both members of the pair are present and cognizant of the parasite loads within a particular successful nest cavity. Second, the parasitic species that take advantage of sequential nests within a season often differ from those that overwinter in nest cavities. That may explain why our results differ from those of Davis et al. (1994), in which Eastern Bluebirds breeding in Kentucky showed a significant preference for boxes containing successful nests from the prior year. Perhaps the number and variety of ectoparasites that overwinter in bluebird nests is low enough that the success-signaling function of nests from the previous year outweighs the parasitism costs of their reuse.

Our results are perhaps best compared to those of Gowaty and Plissner (1997), who also used an experimental procedure to address within-season nest reuse in bluebirds. By comparing the propensity of bluebird pairs to renest in successful cleaned boxes versus successful soiled ones, the authors found that bluebirds more often chose cleaned boxes over uncleaned boxes. However, their results did not achieve statistical significance. They conclude that "if there is a difference in breeding dispersal away from cleaned vs. uncleaned boxes, it is quite small, perhaps smaller than our potential limits of resolution" (Gowaty and Plissner 1997, p. 328). Our results suggest that the weakness of the preference they detected was due to their experimental design rather than a lack of sensitivity on the part of the birds. In their study, alternative boxes were erected after the onset of incubation, and placed at variable distances, up to 200 m, from the initial box. Therefore, by chance alone one could expect half of the boxes to be in poorer microhabitat than the original nestbox. By providing all bluebird pairs with an alternative nest site in the immediate vicinity (<2 m away), our study controlled for the potentially confounding variables of nest-site quality and availability.

Our results indicate that bluebirds operate under two conflicting rules of thumb ("reuse successful cavities" and "avoid soiled cavities"). These in turn are the basis of the two conflicting hypotheses found in the literature concerning nest-site reuse. In our study, aversion to parasites outweighed preference for successful cavities. However, it would be inappropriate to conclude that avoidance of parasites will always outweigh the preference for successful cavities. We purposefully minimized costs of nest-site

switching by providing two boxes side by side. Gowaty and Plissner's (1997) data clearly demonstrate that by increasing the cost of nest-site switching (breeding dispersal), one can alter the nest-site choice eventually made by the birds. Indeed, if the quality of alternate cavities is low enough, one would expect birds to preferentially reuse soiled cavities. Nest-site preferences are thus best considered to be relative rather than absolute.

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