Fecal Sac Removal: Do the Pattern and Distance of Dispersal Affect the Chance of Nest Predation?

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The classic experiment of Tinbergen et al. (1963) on eggshell removal in gulls demonstrated the significance of removing conspicuous objects from around the nest; predators used the color of broken white eggshells as cues for locating and depredating nests when the shells were left nearby. A comparable principle of reduced predator attraction can be extended to the removal of fecal sacs (feces enclosed in a mucous covering), which may attract predators by their odor or appearance (Herrick 1900, Skutch 1976, Welty 1982). However, despite many anecdotal reports of birds transporting nestling fecal sacs from their nests, it has yet to be determined whether the presence of sacs near the nest increases predation of those nests. An alternative hypothesis suggests that removal of feces keeps the nest dry and free of arthropod colonization (Herrick 1900, Blair and Tucker 1941, Welty 1982). Although there is much variability in the degree to which bird species maintain their nests (Welty 1982), the frequency of fecal sac removal in such a diverse group of species suggests that there is selective pressure for sac disposal.

Weatherhead (1984) assumed that fecal sacs attract predators to nests and predicted that birds would disperse sacs widely so that they would not accumulate near the nest. Petit and Petit (1987) and Weatherhead (1984, 1988) showed that Prothonotary Warblers (Protonotaria citrea) and Tree Swallows (Tachycineta bicolor), respectively, did not disperse fecal sacs widely around their nests. Nevertheless, Weatherhead's hypothesis of fecal sac dispersal raises an intriguing question: if fecal sacs attract predators, is there an optimal pattern and distance of dispersal such that cues to predators are minimized?

The purposes of this study were to determine (1) if predators are attracted by avian feces, and (2) if the pattern and distance of fecal sac dispersal are important in concealing the location of the nest from predators.

METHODS
Experiments were conducted in four large (>10 ha) woodlots in Wayne County, Ohio, between 22 July and 15 August 1986. Although most birds in Ohio have completed nesting by late July, we felt that the timing...
of our study would not adversely influence our results. By not having active nests on our plots, we eliminated any bias associated with the possibility of having active nests near experimental eggs. Plot vegetation was dominated by mature stands of red oak (*Quercus rubra*), white oak (*Q. alba*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), shagbark hickory (*Carya ovata*), and white ash (*Fraxinus americana*).

To determine if bird feces attracted predators, we positioned fresh quail (*Coturnix*) eggs (average dimensions 3.07 x 2.51 cm, n = 3) in a 4 x 5 grid pattern. One egg was placed on the ground at each of 20 stations, and, at 10 of them, fresh (< 4 days) chicken feces covered with a white flour and water paste (approximately 25 ml) were situated 10 cm away. Eggs with and without feces were alternated 25 m apart within the grid. The 70-g pile of feces was an approximation of the quantity produced by a single Tree Swallow nestling during the entire nestling period (Weatherhead 1984), or by a brood of four, 5-day-old Prothonotary Warblers in 2-4 days (L. J. Petit, unpubl.). Thus, the quantity of feces we placed around eggs is conservative as compared to the amount produced by an entire brood over the nestling period. The dilute flour and water solution was placed over the feces (and on low (<30 cm) vegetation directly over the feces) to represent the white coloration of many species' fecal sacs. We assumed that the inconspicuous (to us) odor of the flour would not itself attract predators (see below). Egg locations were marked with a small (10 cm) piece of flagging tape placed 1 m away and 2 m above the ground. The grid was checked for signs of egg predation after 7 days. We replicated the experiment seven times, all on different plots. Differences between predation rates of eggs with or without feces were assessed with the Wilcoxon's matched-pairs signed-ranks test. This statistic took into account the variability of predator pressure on the seven different plots.

To provide some insight into the role of white coloration of feces in attracting predators, we set out an additional 10 eggs in one of the woodlots. Eggs were placed 25 m apart and each was 10 cm from a 70-g pile of feces that lacked the flour-water paste covering. If the predation rate of these eggs did not differ from that of eggs placed near feces covered with flour paste, we would have some support for our assumption that the flour itself did not cause idiosyncratic results.

It is important, here, to note the potentially artificial nature of our representation of fecal sacs. Because of the difficulty in obtaining an ample supply of fresh fecal sacs for this experiment, we chose to use readily-available chicken feces. Passerine fecal sacs and our experimental feces (chicken feces and flour paste) are both white, thus there should exist no bias with respect to color. However, the difference in odor, the other potential cue for predators, is unclear. Avian physiologists draw few distinctions among species when referring to composition of excrement (e.g., Shoemaker 1972, Sturkie 1976). Furthermore, almost no information exists on the composition of passerine fecal sacs (but, see Morton 1979). Because nitrogenous wastes comprise the majority of bird fecal material, and because many of those compounds are odoriferous to mammals, it seems that if an important difference existed between chicken feces and passerine feces, it would be due to a discrepancy in nitrogen content. Nitrogen concentration of excrement varies widely among individual fowl, depending on such factors as dietary protein, available water, and exercise (e.g., McNabb and McNabb 1975, Sturkie 1976). We could not locate any information on nitrogen content of passerine feces, but Rock Doves (*Columba livia*) excrete uric acid in proportions similar to that of chickens (e.g., McNabb and Poulsom 1970, Shoemaker 1972, Sturkie 1976). For our purposes, we assumed that chicken feces would attract mammalian predators at least as well as a similar mass of passerine fecal sacs.

The importance of the pattern of fecal sac dispersal and distance was tested by varying the arrangement of feces around the eggs. A 5 x 8 grid was laid out and marked in a fashion similar to those already described. Control eggs (no feces) and four treatments of eggs were positioned in a regular pattern within the matrix: (1) close line (CL)—linear arrangement of feces toward the egg and situated between 1 m and 2 m away; (2) far line (FL)—as above except feces positioned between 5 m and 6 m away; (3) close circle (CC)—circular arrangement (radius = 1 m) of feces around the egg; (4) far circle (FC)—same as CC except radius of 5 m. For all treatments, seven piles of feces, each weighing 10 g, were used. Plots were checked after 7 days.

The linear arrangement of feces represented an extreme case in which parent birds always leave their nests in the same direction and drop fecal sacs close to one another. The circular arrangement of feces simulated a situation where parents varied their departure directions, but dropped sacs about the same distance from the nest on all trips. This experiment was replicated twice (on different plots) giving a total of 16 trials for each of the four treatments and the control. Results were analyzed with log-likelihood ratio (G) tests.

The relationship between predation and distance between feces and eggs was analyzed using PROC NLIN (SAS Institute 1985) for nonlinear regression. For this analysis, control eggs (no feces) on the 4 x 5 grid were considered to be 25 m from the nearest feces.

**RESULTS**

Eggs that were 10 cm from fecal material suffered greater predation (78.6%, 55 of 70) than eggs not near fecal material (5.7%, 4 of 70; t = 0, n = 7, P = 0.01, one-tailed test). We found no significant differences among egg predation rates for each of the four arrangements of feces (i.e., CL, CC, FL, FC) around eggs (G = 3.03, df = 3, P = 0.39, Table 1). Eggs with fecal material placed at 1 m (n = 32) and 5 m (n = 32) were depredated in 31.3% and 15.6% of the cases, respectively (G = 2.21, df = 1, P = 0.068, one-tailed test, Table 1).

Comparisons between circular (n = 32) and linear (n = 32) arrangements of feces disclosed no significant differences in predation rates (G = 0.09, df = 1, P = 0.77, Table 1).

Predation occurred on nine of 10 eggs near feces that were not coated with flour-water paste. This rate of predation was not different from that of those eggs (n = 70) located near (10 cm) flour-covered feces (G = 0.82, df = 1, P = 0.37).

Using data from all experiments, nonlinear regression revealed a significant inverse relationship between...
TABLE 1. Effect of feces arrangement on frequency of egg predation.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Depredated (%)</th>
<th>Not depredated (%)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC</td>
<td>6 (37.5)</td>
<td>10 (62.5)</td>
<td>16</td>
</tr>
<tr>
<td>CL</td>
<td>4 (25.0)</td>
<td>12 (75.0)</td>
<td>16</td>
</tr>
<tr>
<td>FC</td>
<td>2 (12.5)</td>
<td>14 (87.5)</td>
<td>16</td>
</tr>
<tr>
<td>FL</td>
<td>3 (18.8)</td>
<td>13 (81.2)</td>
<td>16</td>
</tr>
<tr>
<td>Control</td>
<td>0 (0)</td>
<td>16 (100)</td>
<td>16</td>
</tr>
</tbody>
</table>

* See text for descriptions of treatments.

frequency of predation and distance between feces and egg \(R^2 = 0.98, F = 310.1, df = 2, 16, P < 0.001, \text{Fig. 1}\).

Shell fragments and disturbed leaf litter at depredated sites indicated that most (approximately 75%) eggs were consumed by mammalian predators, although snakes apparently also took some eggs. Predatory activity followed no apparent pattern with respect to location of treatments within any of the plots.

DISCUSSION

The effort that adults of many bird species expend in promptly removing feces from the immediate vicinity of the nest suggests some selective pressure for this behavior. Following feeding episodes, adults often remain on the nest cup in anticipation of fecal sacs, and may touch the nestling bill (Mayfield 1960) or cloaca (Nolan 1978) to stimulate defecation.

Our results show that the presence of feces near a "nest" may significantly increase the incidence of predation by attracting predators. This leads us to believe that the presence of fecal material near the nest combined with movements of adults and begging calls of nestlings would further enhance the ability of predators to locate nest sites. On the other hand, many passerines build their nests > 1 m above the ground and this may protect the contents even if predators were attracted to the immediate vicinity. However, because of the potentially artificial nature of our "fecal sacs" (see above), our results should be viewed as preliminary. The use of actual fecal sacs placed around or below active nests would provide more definitive results on this topic.

If we assume that feces or other conspicuous objects left around nests do attract predators, as suggested by our results and other studies (e.g., Tinbergen et al. 1963), then our experiment on dispersal patterns demonstrated that the arrangement (at least those used in this study) of fecal sacs around the nest did not have a significant effect on egg predation. This suggests that when dispersing fecal sacs, birds do not have to deviate from preferred foraging pathways, as suggested by Weatherhead (1984), in order to decrease the likelihood of nest predation. This would be a more efficient use of time and energy and would allow birds to proceed directly into favored foraging areas once they disposed of the sac.

Studies to date (Weatherhead 1984, Petit and Petit 1987) have demonstrated that parent birds carry fecal sacs in directions different from where they normally forage. However, for Prothonotary Warblers, this was largely due to these birds dropping sacs over open water, areas where they did not forage, but where fecal sacs would not offer clues to the nest site. Other species also have been reported to drop fecal sacs in water (e.g., Williams 1952, Skutch 1976, Weatherhead 1984). Thus, while the pattern of fecal sac dispersal may not usually be an important factor in reducing the probability of nest predation, birds may deviate from normal foraging pathways to dispose of fecal sacs over water, when available, thereby eliminating attraction of predators to the nest (also see Weatherhead 1988).

Our data suggest that, on our study sites, birds should carry fecal sacs >1 m from the nest to sufficiently decrease the probability of attracting predators to the nest. Although the steepest decline in predation rate occurred between 10 cm and 1 m, 30% of eggs placed at the latter distance still were depredated. Carrying fecal sacs >5 m would reduce the incidence of predation even further, although the amount of reduction becomes smaller with increased distance. Other studies (e.g., Ligon 1970, Anderson and Anderson 1973, Nolan 1978, Weatherhead 1984, Petit and Petit 1987) have shown that woodpeckers and passerines often fly >25 m from the nest before disposing of fecal sacs. Why birds carry sacs such a great distance is unclear and is in need of further study.

Weatherhead suggested that predators may use the white color of fecal sacs to cue in on nest locations. In our study, it appears that odor, independent of color, was used by predators to locate eggs. This may be due to the fact that, on our study sites, predators were mainly mammals. Color may be more attractive to avian predators (e.g., Tinbergen et al. 1963) which can survey the ground or the upper surfaces of white-washed foliage.

Our results support the assumption made by previous researchers that one function of removing fecal sacs from the nest by adult birds apparently is to decrease the probability of nest predation. Additionally, although the patterns of feces dispersal around the nest could not be demonstrated to affect the likelihood of nest predation, removal of feces to a certain distance from a nest can reduce the attraction of predators to that nest.
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LITERATURE CITED

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GREAT BLUE HERON DEATHS CAUSED BY PREDATION ON PACIFIC LAMPREY

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Key words: Great Blue Heron; Ardea herodias; Pacific lamprey; Entosphenus tridentata; mortality; prey induced.

Encounters between predator and prey commonly lead to the death of the prey species; accidental deaths of the predator are believed to be relatively rare. Here we report two cases of Great Blue Heron (Ardea herodias) mortality involving the Pacific lamprey (Entosphenus tridentata) in Alviso, California.

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¼ Current address: U.S. Forest Service, Shasta-Trinity National Forest, Big Bar, CA 96010.

The Great Blue Heron is known for its diversity of diet, attacking almost any mammal, bird, fish, or invertebrate that stands a remote chance of being swallowed (Bayer 1978, Bent 1926, Palmer 1962). However, its ability to capture large and unwieldy prey has on more than one occasion led to the death of the heron. Frogs (Langdale 1897), carp (Ryder 1950), bullheads (Bent 1926), and snakes (Cottam 1938) have been involved in such deaths. To our knowledge the Pacific lamprey has not been previously recorded as a prey species of the Great Blue Heron.

Although diversity typifies the herons’ feeding habits, they are mainly piscivorous. In a study conducted by Willard (1977) of the feeding habits of five species of herons, the Great Blue Heron consistently captured fish that were too large for the other heron species.