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FECAL SAC DISPERSAL BY PROTHONOTARY WARBLERS: WEATHERHEAD'S HYPOTHESIS RE-EVALUATED[1]

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Abstract. Data on removal of fecal sacs by Prothonotary Warblers (*Protonotaria citrea*) were used to test Weatherhead's (1984) hypothesis that birds carrying fecal sacs away from the nest will vary their departure directions more widely than will birds not carrying fecal sacs in order to prevent attraction of predators. We recorded the departure direction of adults and whether or not they carried fecal sacs, as well as the distance flown to drop a fecal sac.

Fecal sacs dropped over land were not carried significantly farther than those dropped over water. Although the distribution of directions flown with fecal sacs was significantly different than that of directions flown without fecal sacs, Prothonotary Warblers did not vary their departure direction more when carrying fecal sacs than when not carrying sacs. In fact, the distribution of trips without fecal sacs was more varied than trips with fecal sacs. Our results contradict the results of Weatherhead (1984), possibly because of differences in data analysis, and do not support his hypothesis of fecal sac dispersal.

Key words: *Fecal sac removal; nest sanitation; predator attraction; Prothonotary Warbler;* Protonotaria citrea.

INTRODUCTION

Many species, particularly passerines, remove nestling fecal material from their nests. Although adults of some species derive nutrients by ingesting nestlings' wastes (Morton 1979), most species carry the material away from the nest. Fecal sacs are easily transported because the excreta are enclosed in mucous coverings. Removal of fecal sacs may be important, for the time and energy spent on their removal could be used for foraging. There are two proposed advantages for removal of fecal sacs: (1) reduced likelihood of arthropod infestation and maintenance of warmth and dryness within the nest (Herrick 1900, Blair and Tucker 1941, Welty 1982), and (2) reduced chance of attracting predators to the nest (Herrick 1900, Skutch 1976). Weatherhead (1984) indirectly tested this latter idea that fecal sacs could be used by predators as cues to locations of nests by measuring departure directions of Tree Swallows (*Tachycineta bicolor*) leaving nests both with and without fecal sacs. He suggested that fecal sacs would be a greater attractant to predators if they were deposited closer to the nest and in a less variably-dispersed pattern. He reasoned that to disperse fecal sacs more widely around nests, departure directions should be more varied in birds carrying fecal sacs than in birds without fecal sacs. Swallows varied their departure directions significantly more when carrying fecal sacs than when not carrying them, confirming Weatherhead's prediction. However, we believe that Weatherhead's analysis was not a true test of his prediction. In this paper, we test Weatherhead's hypothesis using data collected on fecal sac removal by Prothonotary Warblers (*Protonotaria citrea*). We compare our methods of analysis with those of Weatherhead and address the question of adaptive significance of fecal sac dispersal.

STUDY AREA AND METHODS

In 1985, we studied breeding ecology of cavity-nesting Prothonotary Warblers along the Tennessee and Duck rivers in west central Tennessee. These bottomlands are dominated by willow (*Salix* spp.), hackberry (*Celtis occidentalis*), river birch (*Betula nigra*), sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), and buttonbush (*Cephalanthus occidentalis*). Most of the

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data in this study were collected along the Tennessee River where the river averages several kilometers in width. Because of damming, the water level of the rivers is raised during the spring and summer and floods the bottomland timber along the shoreline and on islands.

As part of a larger study on Prothonotary Warblers (Petit 1986), we erected 252 nest boxes, fashioned from 1.9 l (half-gallon) cardboard milk cartons (Fleming and Petit 1986), along the river and on small (1 to 5 ha) islands within the river. Most nest boxes were placed over water (10 to 150 cm deep) and within 20 m of the vegetation/open water interface. Nest boxes were affixed to trees with heavy strapping tape and placed 1.5 to 2.0 m above ground or water.

From 18 May to 14 July, we observed feeding trips by adult Prothonotary Warblers to nest boxes. We positioned ourselves >20 m from the nest box, and we were usually partially concealed by trees or bushes. We varied our position if we watched a given box on more than one date. Because of the above precautions and because Prothonotary Warblers are relatively tame, we do not believe that our presence significantly affected directions in which adults flew when leaving a nest. Each time an adult departed from the nest, we noted direction (N, NE, E, SE, etc.) and whether or not it was carrying a fecal sac. The direction was estimated when the bird had flown 10 m from the nest box. Although the birds did not usually drop their fecal sacs at this distance, once they had flown this far they rarely altered their direction. When possible, we recorded the distance the bird flew before dropping the sac and whether the sac was dropped over land or water. All observation periods lasted 1 to 4 hr, but most were 3 hr long.

Data were analyzed in two different ways. First, we followed the methods as outlined in Weatherhead (1984). Because of differences in absolute departure directions chosen by birds at different nests, we grouped data into eight octants that were expressed as deviations (−2, −1, 0, +1, etc.) from the modal ("preferred") direction for each nest (the direction chosen most often during a given period by birds when they did *not* carry away fecal sacs [see Weatherhead 1984]). The distribution of trip directions with fecal sacs and those without sacs were compared with a chi-square goodness-of-fit test.

Our second analysis was based on circular statistics. We, again, analyzed adult departure directions based on the dispersion of points around a preferred direction. However, we summarized trips with fecal sacs separately from the distribution of trips without sacs; i.e., a preferred direction based upon the direction in which most sacs were carried during any given observation period. Dispersion of the circular data was described by the quantity, r, which measures the degree of concentration of data points (Batschelet 1965). Values of r range from 0 (low concentration; i.e., high dispersion) to 1.0 (high concentration; i.e., low dispersion). Next, we statistically tested for differences in angular dispersion of each data set (trips with sacs vs. trips without sacs) using the nonparametric method described by Wallraff (1979).

RESULTS

We recorded departure directions for 1061 trips without fecal sacs and 412 trips with fecal sacs during approximately 150 hr of observations on 39 nests. Nearly 84% (332 of 397) of the fecal sacs were dropped over water. No significant differences in locations of dropped fecal sacs existed between boxes on land and boxes over water ($P > 0.10$). Mean distance fecal sacs were carried did not differ between those dropped on land ($\bar{x} = 41.2 \pm 15.1$ m SD, $n = 18$) and those deposited in water ($\bar{x} = 39.2 \pm 20.8$ m SD, $n = 103$; $t = 0.39$, $P > 0.50$). Using Weatherhead's preferred direction showed that the distribution of departures with fecal sacs differed from that of trips made without fecal sacs ($\chi^2 = 52.4$, df = 7, $P < 0.001$; Fig. 1A). Likewise, the distributions of the two data sets with separate preferred directions were significantly different ($\chi^2 = 23.0$, df = 7, $P < 0.01$; Fig. 1B).

Using the same preferred direction, the distribution of trips with fecal sacs ($r = 0.50$) was more varied than trips without fecal sacs ($r = 0.69$). However, when the distribution of departure directions for warblers carrying fecal sacs was calculated independently of trips without sacs, there was a higher degree of concentration ($r = 0.79$) than for either of the two aforementioned distributions. This descriptive measure was supported statistically, as the distribution of trips without fecal sacs was more varied than that of trips with fecal sacs ($Z = 3.56$, $P < 0.001$).

DISCUSSION

In contrast to Weatherhead's (1984) findings, fecal sacs dropped over land by Prothonotary War-

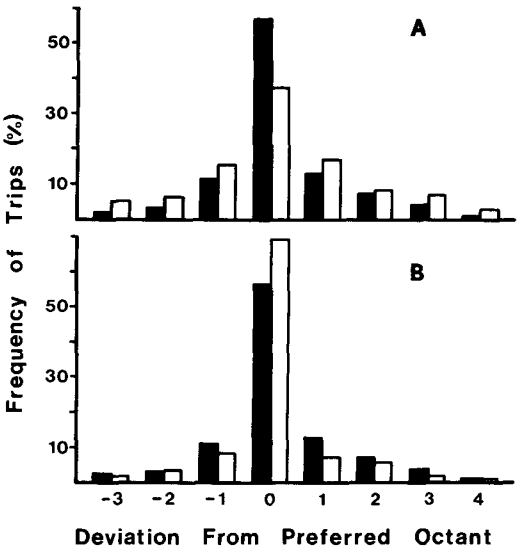

FIGURE 1. Distributions of departure directions for birds leaving the nest with (open bars) and without (solid bars) fecal sacs. Octants are represented by deviations from a preferred direction. Distributions relative to the preferred direction (A) based on trips without fecal sacs and (B) based on their separate preferred directions.

blers were not carried farther from the nest than those dropped over water. Possibly, Prothonotary Warblers carry fecal sacs a predetermined distance regardless of where the sacs are dropped.

When analyzed with a common preferred direction, our data followed a pattern similar to that shown by Weatherhead (1984). That is, trips with fecal sacs were more widely dispersed around the preferred direction than were trips without fecal sacs. This method, however, assumes that preferred directions of trips with and without fecal sacs are always the same. So, Weatherhead actually tested for similarity between distributions of trips with fecal sacs and trips without fecal sacs based on one preferred direction, *not* necessarily whether one sample set varied more widely than the other. In fact, our results from calculating distributions separately showed that departure directions with sacs actually varied less than trips without sacs. Thus, our initial result (using Weatherhead's preferred direction) showing trips with fecal sacs to be more widely dispersed was simply due to Prothonotary Warblers carrying fecal sacs in a direction different than their preferred foraging direction. Often, all quadrats were not available to foraging by the foliage-gleaning Prothonotary Warblers due to open water. Conversely, fecal sacs could be dropped in any area around the nests. Thus, our test of the dispersal hypothesis was liberal, yet we still did not find results that Weatherhead predicted.

Since most fecal sacs were dropped over water, our results are not surprising because sacs dropped in water are transported away or sink to the bottom, and, therefore, do not provide cues to the locations of nests. Although a better test of the dispersal hypothesis would be to use land-nesting birds, Tree Swallows nesting on land did not differ significantly in their departure directions with and without fecal sacs (Weatherhead 1984). However, Weatherhead's method of analysis may have obscured the true relationship in these nests.

Weatherhead (1984) suggested that "there is a cost to removing fecal sacs and that over an entire nesting period, this cost may be of some consequence to breeding birds." Both studies have shown that departure directions from the nest were more varied for birds that removed fecal sacs than they would have been if the birds had not removed wastes. However, the energetic and time costs incurred by birds removing fecal sacs may not be that substantial. For example, assume that a small (14.5 g) passerine carries fecal sacs approximately 40 m from its nest (as in Weatherhead and this study) and that it carries the sacs in a direction directly opposite (i.e., 180°) that of the normal foraging area. Assume, also, that the bird flies 24 km/hr (Welty 1982) and removes, on average, 1.5 fecal sacs/hr for 14 hr each day (this study). Then, by using the equations in Kendeigh et al. (1977) for calculating the cost of flight, we can estimate the additional energetic costs of removing fecal sacs. Under these conditions, the bird would expend only an additional 0.206 kcal/day by removing fecal sacs. This amounts to an increase in energy expenditure of only 2.6% above the existence metabolic rate (EMR; a very conservative estimate of the energy required per day for existence; see Kendeigh et al. 1977). Thus, this analysis suggests that removal of fecal sacs may not be costly in terms of either time (total time spent transporting sacs = 5 min/day) or energy.

Until it can be shown that birds reduce the frequency of nest predation by dispersing fecal sacs widely, or even that fecal material attracts predators, one should not assume that anything more than simply removing wastes from nests is

adaptive. Removing fecal sacs may have its benefits, but whether it is for hygienic reasons or to reduce predation (or both) must be determined by experimental testing.

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