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COMMENTARY

ADAPTIVE DISPOSAL OF FECAL SACS?

Petit and Petit (1987, Condor 89:610–613) recently studied fecal sac disposal by Prothonotary Warblers (*Protonotaria citrea*) to test my hypothesis regarding how birds should dispose of fecal sacs to reduce predation risks (Weatherhead, Condor 86:187–191, 1984). Here I provide support for their conclusion concerning the appropriate analysis of directional data but take issue with several other points raised in their paper.

It is first necessary to establish what hypothesis(es) is under consideration because Petit and Petit refer to "Weatherhead's hypothesis," as though only a single idea is involved, which is not the case. In general, I proposed that birds dispose of fecal sacs adaptively by incurring the minimum costs to carry fecal sacs the distance and direction from the nest necessary to prevent predators using them as a cue for locating the nest. The specific hypotheses I tested in my study of Tree Swallows (*Tachycineta bicolor*) were that swallows nesting over land should carry fecal sacs further and disperse them more widely around the nest than those nesting over water due to water being a superior disposal medium than land. I found support for the first hypothesis but not the second. I also tested the hypothesis that swallows in both habitats should vary departure directions from the nest more when leaving with fecal sacs than without to effect wider dispersal of the fecal sacs. I reported evidence in support of this hypothesis.

My intention, perhaps poorly articulated, had been to propose that all passerines should dispose of their nestlings' feces in a manner that reduced the risk of nest predation, but that the particular way this would be done would vary according to specific circumstances. I can best illustrate this by describing the observation that motivated the Tree Swallow study. While sitting in a suburban garden in Ottawa on a June day in 1980, my attention was drawn to a pair of Common Grackles (*Quiscalus quiscula*) nesting in the garden. Each time either parent departed the nest with a fecal sac they invariably flew into the neighbor's garden and dropped the fecal sac in the neighbor's swimming pool. Foraging trips without fecal sacs were much more varied in direction. After observing seven or eight trips with fecal sacs I entered the neighbor's garden. Both the state of the swimming pool and the state of the neighbor suggested that the grackles had been maintaining this practice for some time. Obviously, in the case of the grackles, deposition of fecal sacs in water required departure directions from the nest to be much more narrowly distributed with fecal sacs than without. In the case of the swallows, I reasoned that the uniformity of the habitat surrounding nests, whether land or water, would render overdispersal of fecal sacs more effective. Thus, specific predictions must be tailored to specific ecological situations.

Petit and Petit applied the specific predictions of the Tree Swallow study to a population of Prothonotary Warblers nesting in boxes, most of which were positioned over water but within 20 m of land. They observed 397 fecal sacs being dropped, 84% of which were dropped over water. Thus, as with the Common Grackles, Prothonotary Warblers did not drop fecal sacs randomly but showed a strong preference for water. Although most of the warbler nests were over water, apparently there were sufficient numbers over land to compare drop distances by birds nesting in both habitats. Petit and Petit reported no significant difference in drop distances but did not indicate the test statistic or the sample sizes for either the number of land nests or the number of drops they observed. If the "land nests" used in this analysis were those positioned on small islands, then presumably the birds were able to drop fecal sacs in water. Therefore, the test would be meaningless as far as comparing the behavior of birds

TABLE 1. Distribution of departure directions from nests by Tree Swallows with and without fecal sacs. The preferred direction is octant 0. Within habitats the only significant pairwise difference is between trips with fecal sacs (0 based on feeding) and feeding trips for water nests ($\chi^2 = 16.44$, df = 5, $P < 0.01$).

	Number of octants from preferred							
	−3	−2	−1	0	1	2	3	4
A) Land nests								
Trips with fecal sacs (0 based on feeding)	4	4	13	29	16	5	2	4
Trips with fecal sacs (0 based on fecal sacs)	4	4	10	38	10	4	4	3
Feeding trips (0 based on feeding)	8	6	27	130	44	16	10	10
B) Water nests								
Trips with fecal sacs (0 based on feeding)	1	8	26	33	11	8	3	3
Trips with fecal sacs (0 based on fecal sacs)	2	7	16	46	8	3	7	4
Feeding trips (0 based on feeding)	6	8	34	139	40	18	7	12

with and without water available for fecal sac disposal, and in no way analagous to the comparison from the swallow study. Even if this result is valid, it in no way changes the fact that Tree Swallows carried fecal sacs over twice as far when nesting over land.

Because of the proximity of land to nests positioned over water, Petit and Petit were able to compare the distances fecal sacs were dropped over land and over water by those birds. Again they reported no significant difference. Sample sizes were provided (total $n = 121$) but it is not explained why the remaining 276 drops that were observed were not included. Ambiguities notwithstanding, Prothonotory Warblers preferentially dropped fecal sacs over water but when dropping fecal sacs over land, they did not fly further.

As explained above, I predicted and reported that Tree Swallows varied departure directions more with than without fecal sacs, particularly for nests over water. In my analysis I determined the preferred departure direction without fecal sacs and then compared the distribution of trips with and without fecal sacs around that direction. Using their data from Prothonotary Warblers, Petit and Petit showed that this method can falsely indicate overdispersion of trips with fecal sacs even if their dispersion is not different, as long as the preferred direction is not the same. A reanalysis of my data for Tree Swallows confirms this result (Table 1). Rather than indicating that swallows vary departure directions more when carrying fecal sacs, these data show that swallows nesting over water change the direction of their departures when carrying fecal sacs. In the case of the warblers, not only did the departure direction change when carrying fecal sacs, the directions of these trips varied less than trips without fecal sacs. Thus, the warblers appear more like the grackles than they do the swallows. Unfortunately, inadequate detail is provided regarding the habitat around the warblers' nests to know whether this result could be due to habitat heterogeneity.

Petit and Petit argued that without direct evidence that fecal sacs attract predators and that fecal sac disposal decreases predation, we should assume that the removal of fecal sacs is nothing more than nest sanitation. While I look forward to seeing studies that examine the effect of fecal sacs on predators, I strongly disagree that we cannot draw inferences about fecal sac disposal from other data. Tree Swallows carry fecal sacs further over land and take them different directions than when they depart the nest without fecal sacs. Prothonotary Warblers show a strong preference for dropping fecal sacs in water (as did one pair of Common Grackles) and they alter both the direction and distribution of departures with fecal sacs relative to departures without fecal sacs. None of these results is expected if fecal sac disposal is nothing but nest sanitation. Caution is not a virtue in science if it results in us abandoning indirect but valid avenues of research.

Finally, there is the issue of the cost of fecal sac disposal. We can only expect habitat variables such as availability of water or predator pressure to influence fecal sac disposal if there is a nontrivial cost to the behavior. Also, if there is no cost, then the decreased clutch sizes of tropical passerines cannot be related to the possibility that tropical species have more elaborate (i.e., costly) patterns of fecal sac disposal (Weatherhead 1984). Petit and Petit estimated that the costs of fecal sac disposal for a small passerine are trivial. Rather than debate their estimate of that cost, I would only point out that birds appear to be sensitive to variation in time and energy when foraging (J. R. Krebs and R. H. McLeery, *In* J. R. Krebs and N. B. Davies, *Behavioural ecology.* 2nd ed. Sinauer, Sunderland, 1984), so I expect the same to be true when they remove fecal sacs.

Financial support was provided by the Natural Sciences and Engineering Research Council of Canada.

PATRICK J. WEATHERHEAD, *Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada.*

The Condor 90:519–521

REPLY TO WEATHERHEAD: A PROBLEM OF INTERPRETING STATED HYPOTHESES RATHER THAN "INTENTION"

In a commentary on our (Petit and Petit, Condor 89: 610–613, 1987) re-evaluation of his fecal sac dispersal hypothesis, Weatherhead (Condor 90:518–519, 1988) expanded upon the ideas presented in his original paper (Weatherhead, Condor 86:187–191, 1984) and confirmed our contention that he unjustly claimed support for one of his predictions. In his more definitive explanation of the "intention" of his original paper, Weatherhead (1988) implied that we misconstrued his hypotheses and that our results with Prothonotary Warblers (*Protonotaria citrea*) cannot be compared directly to his results with Tree Swallows (*Tachycineta bicolor*) because of differences between species and between local habitat structure. In addition, Weatherhead claimed that a number of ambiguities existed in our paper and that we were too cautious in drawing inferences from existing data. Here, we address all of those concerns.

Weatherhead (1988) was confused as to which of his hypotheses we re-evaluated. Although we addressed both of Weatherhead's (1984) main hypotheses (see below), we only *re-evaluated* one of them: that birds should vary their directions more when leaving the nest with fecal sacs than when departing the nest without fecal sacs (the "directional" hypothesis). We clearly stated this in the first sentence of our Abstract and in our Introduction. Also, we allocated only *42 words* in our discussion to the question of "distance," whereas the "directional" hypothesis was given *>six times* that attention. We did not re-evaluate or question Weatherhead's analysis of drop distances, only his interpre-