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.

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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-

tation of departure directions. Thus, there should be no uncertainty as to the major focus of our report.

Weatherhead argues that the "intention" of his original work was "to propose that all passerines should dispose of their nestlings' feces in a manner that reduced the risk of nest predation, but the particular way this would be done would vary according to specific circumstances." We have no argument with *this* reasoning. However, Weatherhead (1984:187) made two *specific* hypotheses: (1) "that Tree Swallows (*Tachycineta bicolor*) nesting over water carry fecal sacs shorter distances from the nest . . ." as compared to birds nesting on land, and (2) "that swallows should vary their departure directions from the nest more when carrying fecal sacs than when not in order to disperse the sacs more widely around the nest." Weatherhead (1984) then applied these hypotheses to *all* passerines: "*A bird has two ways* [italics ours] in which to deposit fecal sacs near its nest so as to lessen their value as cues to nest location by a predator. First it can drop them farther away from the nest and second, it can vary the direction from the nest that they are dropped. Tree Swallows apparently employ both tactics." There was no mention of dispersal tactics varying among species or under different circumstances. Weatherhead (1988) correctly stressed that his general idea, stated in his commentary, must be tailored to different ecological situations. We agree with this statement, but had no way of knowing his "intention" when it was not stated. Nevertheless, Weatherhead's (1988) clarification and expansion of his original ideas in no way invalidates our re-evaluation of his directional hypothesis. We showed that his analysis was not an appropriate approach in assessing his prediction and both our results and Weatherhead's (1988) re-analysis of his data showed that neither species varied their direction more when carrying fecal sacs than when leaving the nest without sacs.

Weatherhead (1988) hypothesized that the supposed homogeneity of habitat surrounding his Tree Swallow nests would cause overdispersal of fecal sacs. He also contended that we provided an inadequate description of habitat surrounding Prothonotary Warbler nests, such that one would not know if a heterogeneous environment around those nests may have caused the difference in feces dispersal between the two species. However, we did provide an in-depth description of the habitat in which we conducted our study and referenced a work which further described our study area. To assess the possibility that Weatherhead raised would require an in-depth quantitative analysis of habitat around each nest box. Although this type of information is important in future research, it was far beyond the scope of our paper. Furthermore, a comparison between studies was impossible because Weatherhead (1984, 1988) provided absolutely no details of the habitat on his study site. Thus, we are left to wonder if the Tree Swallow boxes were positioned in field or forest and whether the water source available was a lake, river, stream, or swimming pool.

Weatherhead (1988) disagreed with our cautious approach to deciphering the proximate and ultimate cause(s) of fecal sac removal. Although we do believe that feces removal from nests of passerines probably is due to nest sanitation, predation, or both (Petit and Petit 1987), we advocated a cautious approach because of the limited knowledge on this topic. For instance, there have been no published studies that have determined whether or not feces even attract predators. The idea that nestling feces left in the nest may increase the chance of nest predation is not new (e.g., Herrick, Auk 17:100–103, 1900; Skutch, *Parent birds and their young,* Univ. Texas Press, Austin, 1976) and is certainly a viable hypothesis. However, relating nestling fecal sac removal to both predation pressure and significantly increased energetic demands on the parents, and then placing this in the evolutionary context of reduced clutch sizes for certain tropical and temperate species appears to be a bit premature. We believe that it is preferable to have at least baseline data on the effects of fecal material on predator attraction and on estimates of the extra energy needed to dispose of fecal sacs *before* certain hypotheses are advanced. Caution *is* a virtue in science when no basic evidence exists for a foundation from which reasonable avenues of research can be pursued.

Weatherhead (1988) questioned our estimate of the cost of fecal sac disposal, but he provided no evidence in support of his opinion. Weatherhead proposed that there must be a significant energetic cost to fecal sac removal if environmental factors, such as predator pressure, are the forces "driving" this behavior. This statement is not necessarily true. In this instance, the "cost" is assessed to the parents if fecal sacs are *not* removed; i.e., predators are more likely to find the nest or nestlings will perish because of unsanitary conditions. Thus, patterns of fecal sac disposal may be the outcome of *benefits* that parent birds receive rather than costs that they absorb. Weatherhead's second argument for the cost of fecal sac removal rests on his previous (Weatherhead 1984) speculation that tropical species have more costly means of ridding the area around their nests of fecal material and that this additional energetic cost may result in decreased clutch sizes of tropical species. This hypothesis was based on the fact that *one* tropical species, the Superb Lyrebird (*Menura novaehollandiae*), carries fecal sacs up to 100 m from the nest and, also, buries nestling fecal material on occasion (Skutch 1976). Weatherhead (1988) reasoned that this hypothesis could be true only if there is a nontrivial cost to removing fecal sacs from the nest. Obviously, more information is needed on fecal sac removal by temperate and tropical birds before this idea can be validated. Finally, Weatherhead (1988) cited the commonly-held belief that birds forage "optimally" and that this optimality can be extended to fecal sac dispersal. Thus, Weatherhead implied that, even if one accepted our small estimate of the cost of fecal sac removal by small passerines, this added energetic demand may still have repercussions on a bird's reproductive output. We do not question that there exists a set of "best" decisions available to birds, but how tightly those decisions are tied to natural selection remains debatable (e.g., Myers, p. 216–221. *In* A. H. Brush and G. A. Clark, Jr. [eds.], *Perspectives in ornithology,* Cambridge Univ. Press, Cambridge, 1983). We recommend that future investigators concentrate on benefits, rather than costs, of fecal sac disposal.

Several trivial problems with our presentation were suggested by Weatherhead (1988). He asserted that *if* Prothonotary Warblers nesting on land in our study had access to water then our test of his "distance" hypothesis was meaningless because one must compare groups with and without access to water. The fact that all of our nests were "water nests," according to Weatherhead's (1984) definition, was made clear in our original manuscript (Petit and Petit 1987:611–612): "Most nest boxes were placed over water . . . and within 20 m of the vegetation/open water interface." and "Although a better test of the dispersal hypothesis would be to use land-nesting birds. . . ." Thus, Weatherhead's contention that we may not have used true land nests was acknowledged in Petit and Petit (1987). Also, we never stated that no significant difference was found for *drop distances* when comparing land-nesting warblers and birds nesting over water (see Weatherhead 1988). What we did analyze was the location (i.e., land vs. water) of fecal sacs dropped by birds nesting in both "habitats" ($\chi^2 = 1.8$), not their drop distances. We realized that we did not have "true" land nests and, therefore, a comparison of distances fecal sacs were carried by the two groups would not be a valid test of Weatherhead's (1984) distance hypothesis. Furthermore, our results showed that birds nesting within 20 m of the land/water interface did not carry fecal sacs farther when they dropped them over land as compared to their flights over water. This is still contradictory to Weatherhead's prediction.

Finally, Weatherhead (1988:519) stated that one of our reported sample sizes for distances was ambiguous because "it is not explained why the remaining 276 drops that were observed were not included." Unfortunately, Weatherhead must have overlooked our Methods section: "*When possible* [italics ours], we recorded the distance the bird flew before dropping the sac . . ." (Petit and Petit 1987:611). This procedure and subsequent omission of those unobserved fecal sac drops in analyses of drop distances were identical to methods used by Weatherhead (1984).

Weatherhead's (1984) original paper was an insightful and stimulating approach to the study of a common behavior that previously had been examined only anecdotally in the literature. We agree with Weatherhead that more research is needed on the costs and, especially benefits, of fecal sac removal. Hopefully, other investigators will use this exchange in a positive manner so that the question of adaptive significance of fecal sac removal can receive the attention it deserves.

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