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FECAL SAC REMOVAL BY TREE SWALLOWS: THE COST OF CLEANLINESS

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ABSTRACT.—Fecal sac removal by Tree Swallows (*Tachycineta bicolor*) was monitored for 10 "land" nest boxes (>100 m from water) and 13 "water" nest boxes (adjacent to or over water). The mean distance from the nest at which "land" birds dropped fecal sacs was more than double that for "water" birds. Departure directions for birds carrying fecal sacs were more variable than for birds not carrying fecal sacs although, contrary to prediction, "land" birds were not more variable than "water" birds. Combining data on the removal rate and weight of fecal sacs over the nestling period produced the estimate that for each nestling, parents removed 70 g of feces in 168 trips. It is hypothesized that where predation pressure requires more time and energy to be spent in disposing fecal sacs, clutch size will be smaller.

In many species of birds with altricial young, the nestlings' feces are enveloped in a mucous membrane and the parents carry that "fecal sac" away from the nest. Although the removal of fecal sacs has been reported anecdotally (e.g., Thomson 1935, Smith 1942–1943, Wible 1960, Skutch 1976), it has never been seriously investigated. In this paper I consider why birds remove fecal sacs, present tests of hypotheses regarding the factors that should influence where fecal sacs are dropped, and discuss the costs to the parents of transporting fecal sacs.

Welty (1982) offered a reasonable explanation for the adaptive function of removing fecal sacs. He suggested that keeping the nest clean of feces helps keep it warm, dry, and free of insect infestation, while transporting the feces away from the nest reduces the likelihood that predators can use them as a cue in finding nests. Although the latter assumption lacks direct support, it receives indirect support from Tinbergen et al.'s (1963) experiments with egg shells and Common Black-headed Gull (*Larus ridibundus*) eggs. They determined that the parents normally remove the shells of hatched eggs from the vicinity of the nest because the bright white interior of the shell attracted predators to the remaining eggs in the nest. The bright white appearance of fecal sacs presumably acts in the same way.

Given that some birds carry fecal sacs away from the nest to avoid predation, one can predict the factors that should be important in determining where the birds drop the sacs. I assume that fecal sacs become more important as clues to predators for locating nests the closer they are to the nest and the more they last and accumulate in the environment around the nest. I first tested the hypothesis that Tree Swallows (*Tachycineta bicolor*) nesting over water carry fecal sacs shorter distances from the nest because water is better than land for dispersing fecal sacs. My second hypothesis was that the swallows should vary their departure direction from the nest more when carrying fecal sacs than when not in order to disperse the sacs more widely around the nest. Furthermore, this greater variation in departure direction should be more pronounced for birds nesting over land than for those nesting over water, for the same reason as before.

Underlying these hypotheses, I assumed that the transport of fecal sacs has some cost to the parents. In order to provide a basis for discussing what these costs might be I present quantification of the frequency and weight of fecal sacs transported during a complete nesting sequence.

METHODS

I conducted my study from May through July 1982 on a population of Tree Swallows breeding in artificial nest boxes located within 10 km of the Queen's University Biological Station in eastern Ontario, 40 km north of Kingston. Thirteen "water" boxes (either adjacent to or over water) and 10 "land" boxes (>100 m from water) were selected for detailed observation.

Once the eggs had hatched in these nests I began observations and continued until either chicks had fledged or the nest failed completely. A nest was observed for 20–40 min (usually 30 min) once per day with the time of day varied regularly. All observations were made between 09:00 and 16:00. During an observation the observer stood approximately 30 m from the nest box and used a spotting scope trained on the nest hole to determine if an emerging bird was carrying a fecal sac. With

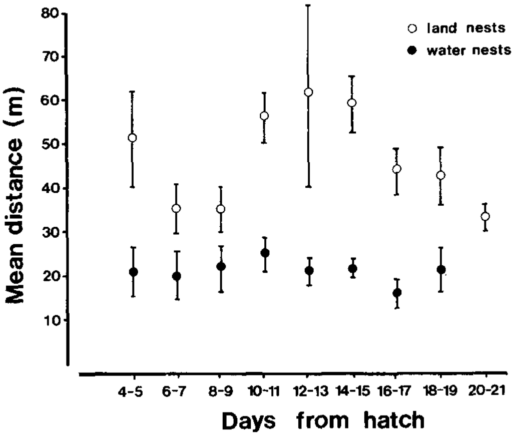

FIGURE 1. Two-day mean distances at which fecal sacs were dropped from nests over land and over water relative to nestling age. Bars show standard error.

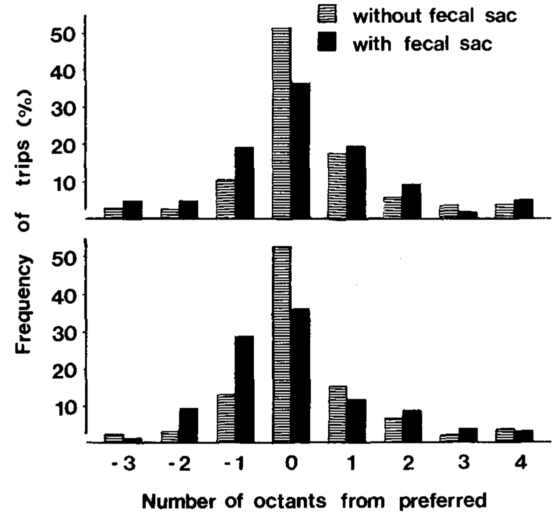

FIGURE 2. Distribution of departure directions from the nest by birds with or without fecal sacs. Octants are defined by their position relative to the preferred foraging direction (octant 0). Upper figure is for land nests and lower figure is for water nests.

the use of binoculars, the observer followed the departure of parents away from the nest. The direction of departure to the nearest octant (e.g., N, NE, E, etc.) was recorded both for trips with and without fecal sacs. The distance from the nest that a fecal sac was dropped was estimated by using the measured distances to landmarks (stumps, shrubs, etc.) as references. Occasionally the place where the sac was dropped could not be determined and these observations were used only for the analysis of departure directions.

Following each observation period, the nest box was opened and the number of nestlings recorded. In addition, each nestling was removed in order to stimulate it to void a fecal sac. Each sac so obtained was individually stored in a sealed vial until its wet weight could be determined later that day.

RESULTS

Approximately 60 h of observation were accumulated over 123 observation periods. During that time the water-nesting swallows made 264 trips without fecal sacs and 93 trips with fecal sacs while the land nesters made 251 trips without fecal sacs and 82 trips with fecal sacs. Ninety-two drop distances were recorded for water-nesters and 59 distances for land-nesters. The mean drop distance for land-nesters (50.25 ± SD 20.87 m) was more than double that (21.32 ± SD 10.40 m) for water-nesters ($t = 11.31$, $P \ll 0.001$; Fig. 1), supporting the first hypothesis. This difference may have been underestimated because substantially fewer birds departing from land nests with fecal sacs were observed dropping them and it is reasonable to assume that the farthest drop locations would be the hardest to see. Although actual foraging distances were not estimated, birds in both habitats regularly foraged farther than 50 m from their nests, so the difference in drop distances cannot be attributed to differences in foraging distances.

Whenever a swallow departed from the nest carrying a fecal sac, it apparently flew to a foraging area after dropping the sac (as opposed to making a special trip to dispose of the sac). Therefore, by comparing the distribution of departure directions for birds going to forage with or without sacs, I could determine whether departure directions were more variable for birds carrying fecal sacs and whether this effect was more pronounced for land-nesters. To account for changes between observation periods in the preferred foraging direction, for each observation period I defined the preferred foraging direction as that chosen most frequently when a bird departed without a fecal sac. I then scored the frequency of departures both with and without fecal sacs in each octant during that observation period. Rather than using fixed octants (e.g., N, NE, etc.) I defined each octant by its position relative to the preferred octant (e.g. −1, +2, etc., where 0 is the preferred octant).

This analysis revealed a similar pattern of fecal sac disposal in the two habitats (Fig. 2). In both cases swallows carrying fecal sacs dispersed more widely than those without sacs. Although the overall distribution of trips with and without fecal sacs did not differ significantly ($\chi^2 = 8.59$, df = 6, $P > 0.05$) for land-nesters, trips with fecal sacs were significantly

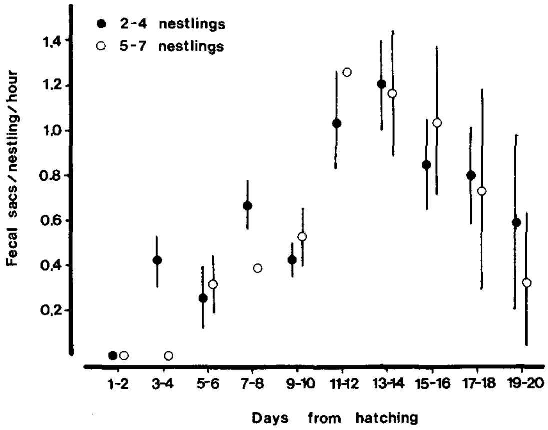

FIGURE 3. Mean per nestling rate of fecal sac disposal. Bars show standard error.

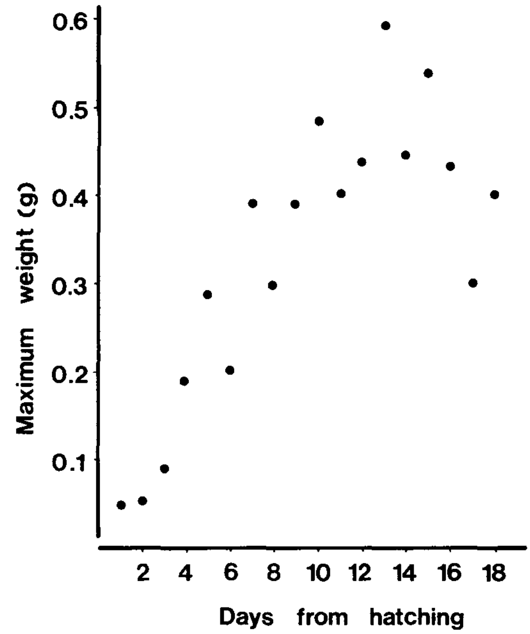

FIGURE 4. Maximum weight (=mean of three largest sacs collected on a given day) of fecal sacs over the nestling period.

fewer than expected in the preferred direction ($\chi^2 = 5.73$, df = 1, $P < 0.02$). For water nests the overall distributions of trips with and without fecal sacs were significantly different ($\chi^2 = 17.34$, df = 6, $P < 0.01$).

The distribution of foraging trips without fecal sacs in the two habitats did not differ significantly ($\chi^2 = 2.36$, df = 7, $P > 0.05$). Therefore, to test the hypothesis that land-nesters should vary the direction of trips with fecal sacs to a greater extent than water-nesters, it was possible to compare directly the distributions of trips with sacs in the two habitats. Contrary to this prediction, the distributions did not differ significantly ($\chi^2 = 3.42$, df = 5, $P > 0.05$).

The pattern of fecal sac removals per nestling per hour, although variable, was consistent between small (two to four nestlings) and large clutches (five to seven nestlings) (Fig. 3). Although there was no reason to expect a difference, it was possible that some interrelationship between brood size and individual energy demands (e.g., Royama 1969) could have caused the rate of fecal sac production per nestling to vary with brood size.

Removal of the sacs occurred in three distinct phases. During the first three days after hatching, no fecal sacs were removed. This was not because none were produced but because it is usual for parents to consume fecal sacs during the early nestling period (Welty 1982). In the second phase, the rate of removal increased rapidly until day 14. This period corresponds to the phase of rapid growth (Ricklefs 1967) and therefore high food consumption. The final phase was marked by a sharp decline in removal rates from day 14 to 20. This pattern primarily reflects the nestlings' deteriorating ability to produce proper fecal sacs, as evidenced by the rapid accumulation of feces in the nest during this time.

The fecal sacs voided by nestlings in response to handling probably weighed less than those voided naturally. Therefore, rather than use the weights of all fecal sacs collected to determine the pattern of weight change with nestling age, I computed the daily value as the mean of the three heaviest sacs collected on that day. While this probably still underestimated the weights of fecal sacs, it did so to a lesser extent than if all weights were used. The weights of fecal sacs increased 12-fold between 1 and 13 days after hatching and apparently decreased after that time (Fig. 4). Because the sacs deteriorated in the late nestling period, it became difficult to collect proper fecal sacs for weighing. The values for days 17 and 18 in Figure 4 are both the weights of single fecal sacs. No weights were obtained for fecal sacs on day 19 or 20 even though observations indicated that they were still being removed (Fig. 3). Thus, the sharp decline in weights shown in Figure 4 may not have been really so pronounced.

To calculate the total weight of feces removed per nestling per day required combining the data in Figures 3 and 4. For a given day I assumed the removal rate to be the mean of the rates for small and large broods. I multiplied this mean by fecal sac weight for that day to provide the weight of feces produced per nestling per hour. Finally, I multiplied the

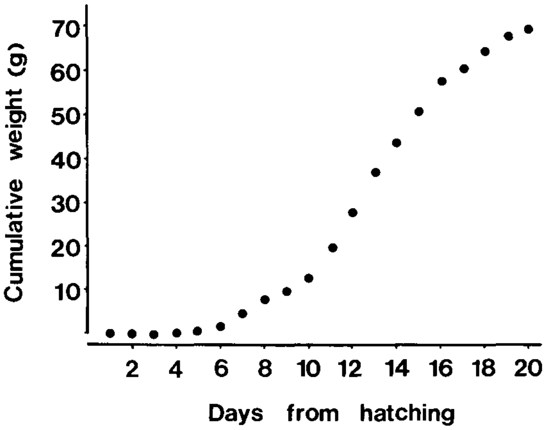

FIGURE 5. The cumulative weight of fecal sacs produced per nestling over the nestling period.

hourly rate per nestling by the estimated 14-h daily feeding period to give the per nestling daily fecal weight. Two exceptions should be noted: since no fecal sacs were seen being removed on day 3, I used a rate of 0; since no fecal sac weights were obtained for days 19 and 20 but fecal sacs were seen to be removed, I used the weight value for day 18 (0.4 g) for days 19 and 20. Over the nestling period, for each nestling the parents removed a total of approximately 70 g of feces in 168 trips (Fig. 5).

DISCUSSION

A bird has two ways 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. They increased the drop distance when dropping fecal sacs on land, compared to drops over water; over both land and water they varied their departure direction more when leaving the nest with fecal sacs than when leaving without them. The swallows did not vary departure directions with fecal sacs more when over land than over water. The last result is perhaps not surprising, however, since by maintaining the same angular variation for drops over land as over water, but doubling the mean distance, the land area over which the fecal sacs were dropped was greatly increased; therefore, the density of fecal sacs in the nest vicinity was greatly reduced.

Two principal costs are associated with transporting fecal sacs, one related to the distance carried and the other to the direction. If a bird carries a sac in the direction it is going to forage, its only cost is a slight increase in wingloading due to the weight of the fecal sac. Its flight efficiency may also be reduced because of drag from carrying a fecal sac in an open bill and shifting the center of balance forward. These costs increase the farther the sac is carried, but, due to the small weight and size of fecal sacs, will be minimal. If, however, a bird carries a fecal sac in a direction other than that in which it will be foraging, it incurs not only the cost of flying a certain distance with slightly greater wingloading and lower flight efficiency, but also, after dropping the sac, the cost of getting itself back to its flight path for foraging. The farther the sac is carried, the greater the distance back to the foraging flight path, and therefore the greater the cost. More information is required before exact costs can be calculated accurately. My aim was only to suggest 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.

Higher costs of disposing fecal sacs may mean that fewer young can be reared. In a sample of 58 land nests and 43 water nests in the study area (D. Leffelaar, pers. comm.), water nests had a significantly larger mean clutch than land nests (5.77 vs. 5.38, $t = 2.22$, $P < 0.05$). Although this difference is in the predicted direction, one cannot say to what extent the difference in clutch sizes can be attributed to differences in the cost of fecal sac disposal in the two habitats (as compared, for example, to food availability). Where disposal costs are high, however, one might expect greater reductions in clutch size associated with them. Skutch (1976) reported that female Superb Lyrebirds (*Menura novaehollandiae*) will fly up to 100 m to deposit fecal sacs in streams, and where no streams are available, will bury the sacs. The total cost of this behavior in time and energy over an entire nesting effort, cannot be considered trivial. It may be noteworthy that females of this species lay only a single egg per clutch (Slater 1974).

The suggestion that the cost of avoiding predation can be a cause of small clutch size is not novel (Skutch 1949, Cody 1966), although the disposal of fecal sacs has not hitherto been invoked as part of that cost. Skutch (1949) suggested that the smaller clutches of tropical birds may be a consequence of the birds' having to visit the nest less frequently in order to avoid exposing the nest location to the abundant (relative to temperate latitudes) predators. If predation is higher in the tropics, or only if predator-prey relationships are more highly coevolved, then tropical birds with altricial young may have to expend more energy disposing of fecal sacs than their temperate counterparts;

these higher costs may account in part for their smaller clutch sizes. More data on fecal sac disposal behavior in both tropical and temperate species will be required before this hypothesis can be assessed.

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