Parental consumption of nestling feces: good food or sound economics?

Parent birds generally eat their nestlings' feces when the nestlings are young and carry the feces from the nest as the nestlings get older. This change in behavior may be due to the decline in energy content of the feces as the nestlings' digestive system becomes more efficient, or because the cost to the parent from eating nestling feces increases with the volume and number of fecal sacs eaten. In tree swallows (*Tachycineta bicolor*), red-winged blackbirds (*Agelaius phoeniceus*), and American robins (*Turdus migratorius*), parents ate a smaller proportion of fecal sacs as their nestlings got older, even though the energy density of fecal sacs remained constant with nestling age. The increase in size of fecal sacs with nestling age explains the decline in parental consumption much better than does energy content. These results better support the hypothesis that eating fecal sacs is an economic alternative to carrying them from the nest and is not done so that parents use the sacs as a source of energy. The benefits of not carrying a fecal sac from the nest may be that parents can remain at the nest longer for other purposes (e.g., brooding) and that they avoid the transportation costs associated with fecal sac disposal. Understanding the costs and benefits of fecal sac consumption may explain both intersexual and interspecific differences in this behavior. *[Behav Ecol 1991;2:69–76]*

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Many species of birds (Blair and Tucker, 1941) and mammals (Ewer, 1968) consume the feces of their young. This is presumably to aid in concealing the young from predators (Ewer, 1968; Weatherhead, 1984) in addition to serving a sanitary function. Avian feces have been demonstrated to attract predators to artificial nests (Petit et al., 1989). Since the feces of nestlings are enveloped in mucosal sacs, parent birds have the option of carrying the feces away from the nest for disposal rather than consuming them. Here we test predictions of two alternative hypotheses proposed to explain why parents sometimes eat fecal sacs and at other times carry and drop the sacs away from the nest.

The observation that parental consumption of fecal sacs declines with nestling age (Blair and Tucker, 1941; Tucker, 1942) and the likelihood that nestling digestive efficiency increases with age (Herrick, 1900) have led to the suggestion that parents eat fecal sacs for their nutritive value (Gluck, 1988; Morton, 1979). For our purposes we will equate energy with nutrition, since parents feeding nestlings will have very high energy demands. Thus, parents eat sacs when the sacs are nutritious and carry them from the nest when they are not (i.e., the decision of whether to eat a fecal sac is independent of any other aspect of parental care). Morton (1979) estimated that fecal sac consumption may provide up to 10% of the white-crowned sparrow (*Zonotrichia leucophrys*) parents' daily energy expenditure. Gluck (1988) found that the energy density (joules/g) of fecal sacs produced by nestling European goldfinches (*Carduelis carduelis*) declined significantly with nestling age, as did the rate of fecal sac consumption by parents.

An alternative hypothesis is that parents eat fecal sacs as an economically superior alternative to carrying the fecal sacs away from the nest, independent of any change in the nutritional value of fecal sacs (i.e., fecal sacs are not eaten for nutritional reasons but because other parental activities sometimes make the benefit of eating fecal sacs exceed the cost). Quinney (1986) estimated that a brood of six tree swallows (*Tachycineta bicolor*) produces approximately three fecal sacs per hour. Carrying this many fecal sacs for distances of well over 50 m from the nest, and in directions other than those in which the parents would ordinarily travel when only foraging, should result in nontrivial time and energy costs to the parents (Weatherhead, 1984, 1988). Consuming fecal sacs also enables the parent to remain at the nest after a feeding bout to tend

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to other needs of the chicks such as brooding and removing ectoparasites. However, while we assume that eating fecal sacs saves the parents transportation costs, consumption will have costs of its own. Even if fecal sacs have some nutritional value, they do contain the digestive and excretory wastes of the nestlings and thus seem likely to tax the parents' digestive tract when they are consumed. Because fecal sac size increases with nestling size and the frequency of fecal sac production varies with feeding frequency, the cost of consuming fecal sacs will also increase with nestling age. This increased cost could also account for the decline in fecal sac consumption by parents as their nestlings get older. Furthermore, as the need for brooding diminishes and the feeding rate increases, parents would need to spend less time at the nest and more time foraging as nestlings get older.

To test these two hypotheses we observed how parent American robins (*Turdus migratorius*), tree swallows, and red-winged blackbirds (*Agelaius phoeniceus*) disposed of their nestlings' fecal sacs, and we assessed the nutritional value of the fecal sacs throughout the nestling period. We chose these three species because of their abundance in the study area and the ease of observation. Nestlings of all three species are fed primarily insects (Hamilton, 1940; McNicol et al., 1982; Quinney and Ankney, 1985; Hurd PL, Weatherhead PJ, and McRae SB, personal observations) and develop at similar rates (although tree swallow nestlings remain in the nest longer, as is typical of cavity-nesting species).

If parents eat fecal sacs for their nutritional value, we predicted that, within species, the proportion of fecal sacs eaten should vary directly with their nutritional value. We also predicted that interspecific variation in fecal sac consumption should be correlated with nutritional value such that the species with the most nutritious fecal sacs ate the highest proportion and the species with the least nutritious sacs ate the lowest proportion. Conversely, if fecal sac consumption is simply an economical way of disposing of fecal sacs when the cost of eating them is affordable, we predicted that in all species the proportion of fecal sacs eaten should be better correlated with fecal sac weight (i.e., smaller sacs are more likely to be eaten) than with changes in nutritional value. Furthermore, we expected that the behavior of a parent that eats a fecal sac should differ from that of a parent that carries a fecal sac (e.g., it may remain at the nest longer or be more likely to brood the young).

METHODS

We conducted this study at the Queen's University Biological Station in eastern Ontario, Canada. All the observations of fecal sac disposal by robins were collected as part of another study (Weatherhead and McRae, 1990) in 1987 and 1988, and all the observations of tree swallows and red-winged blackbirds were made in 1989. Fecal sacs used for analysis from all three species were collected in 1989. Weather data for 1987 and 1988 were provided by the Atmospheric Environment Service from their weather station at Godfrey, 20 km from the Biological Station. Weather data for 1989 were obtained from a weather station that was installed at the Biological Station.

Behavioral observations

With the exception of one robin nest observed from a blind, we collected all behavioral data by videotaping nests. Videotaping was superior to direct observation for several reasons. First, the birds usually appeared oblivious to video cameras in contrast to their strong response to human observers. Second, observing behavior using videotape is facilitated by the capability to view the tape in slow motion and to review behaviors that are not clear. Finally, with four cameras we were able to collect data from several nests simultaneously.

Robin nests were videotaped by placing the tripod-mounted camera 1–4 m from the nest. Taping was done between 0700 and 1800 h varying the days of the nestling period each nest was filmed. We chose nests opportunistically based on accessibility and favorable lighting conditions. All robin parents were individually color-banded. Using video cameras, we recorded 149 continuous observations averaging 88 min (SD = 46 min) at 23 nests.

All the red-winged blackbird nests we observed were located in marshes. We placed the video camera 1–3 m from the nest if cover was available and 7–10 m from the nest when there was no cover. We recorded 28 continuous observations from 18 nests lasting a mean of 203 min (SD = 97 min).

All tree swallow nests were in nest boxes. Each box had one side made of glass to facilitate videotaping. We normally kept the glass covered with dark plastic. When filming, we removed the plastic and placed the camera lens against the glass. The remaining exposed glass was then covered with plastic to avoid any glare. The light entering the box through the opening used by the birds was adequate to allow videotaping. We covered the camera with a burlap blind to minimize its novelty. When filming was completed, the camera was removed, the window in the side of the box was recovered with plastic, and the blind was left in place so the birds remained familiar with it. All parent swallows were banded and

uniquely marked with acrylic paint to facilitate identification. We collected 24 continuous observations from seven nests lasting an average of 266 min (SD = 98 min). After tree swallow nestlings reach 10 days of age, their parents carry all fecal sacs away from the nest (see below). Therefore, we made no further observations after the tenth day posthatching.

Tree swallow and American robin nestlings could easily be seen producing fecal sacs. Before voiding, nestlings typically lowered their heads and raised their cloacas, prompting parents to position themselves to grasp the fecal sacs directly from the cloacas. Because of the distance of the cameras from red-winged blackbird nests and because the angle of the camera relative to the nests was lower, we had more difficulty observing the fecal sacs being produced. However, the sacs were readily observed in the parents' bills. Consumption of fecal sacs by parents of all three species was also unambiguous, because the parents typically tilted their heads backward and could be seen swallowing. After swallowing a fecal sac the parents often remained at the nest for a further period of time. In contrast, when sacs were carried from the nest the parent departed from the nest immediately upon grasping the fecal sac in its bill. Those few cases in which the method of disposal was not known with confidence after repeated viewing were discarded. Using the timers built into the cameras, we recorded the duration (to the nearest minute) of nest visits when fecal sacs were eaten. For robins we recorded the total duration of the nest visit, whereas for red-winged blackbirds and tree swallows we only recorded the time spent at the nest after the sac was eaten. While this makes these observations for robins not directly comparable to the observations for the other two species, relative changes within species are comparable. Furthermore, only about 1 min of each robin visit elapsed up to the time the fecal sac was eaten.

Fecal sac analysis

To collect fecal sacs we removed nestlings from the nest. This handling was usually adequate to stimulate red-winged blackbird and tree swallow nestlings to void a fecal sac if they had a fecal sac available (fecal sacs are easily seen through the nestlings' skin). We were able to position vials so that fecal sacs were voided directly into the vials. Vials were immediately labeled and sealed, and within 3 h they were frozen. Overall we collected 104 red-winged blackbird fecal sacs from 46 nests and 75 tree swallow fecal sacs from 34 nests.

After the robin nestlings were 5 days old, we were able to collect fecal sacs from the nestlings by the same method described above. Before 5 days, however, robin nestlings do not reflexively defecate on handling. To collect fecal sacs from young robin nestlings we removed nestlings from the nest one or two at a time. We fed them pieces of earthworm, which usually resulted in their voiding a fecal sac within several minutes. When voiding a fecal sac, the nestlings first raised their cloacas, allowing us to position a vial under the cloaca to collect the fecal sac. We then replaced the nestlings in their nests and did not resample from them for at least 24 h. We collected a total of 79 robin fecal sacs from 12 nests.

We freeze-dried fecal sacs for 3 days before weighing them, then ground them to a powder using a Wig-L-Bug amalgamator (Crescent Dental Mfg. Co., Chicago, Illinois). We took subsamples from the powdered sac and pressed them into pills using a hammer and pellet maker. Between one and 20 pills were made from each sac, except for the case of very small sacs (see below). We then freeze-dried the pills for a further 3 days before subjecting them to bomb calorimetry using a Phillipson (Phillipson, 1964) Oxygen Microbomb Calorimeter (Gentry Instruments, Inc., Aiken, South Carolina). We measured both the energy density (j/mg dry weight) and the percentage by weight of incombustible material in each sac subjected to calorimetry. The former value represents the maximum energy potentially available to a parent eating a fecal sac, whereas the latter represents the minimum amount of a fecal sac from which no energy could be obtained.

More fecal sacs were collected than we could use for calorimetry (12 sacs took 10 days to process). We subsampled sacs by randomly choosing four sacs for each age of nestling per species. In the case of very young nestlings, where single fecal sacs were too small to form a pill, we combined enough sacs to produce one pill. In several cases we only had enough fecal sacs from young nestlings to produce one or two pills for a given age. In total, 44 tree swallow sacs from 27 nests, 39 red-winged blackbird sacs from 22 nests, and 43 American robin sacs from 11 nests were subjected to calorimetry.

We analyzed all the data using the Statistical Package for the Social Sciences (Nie, 1988). All correlations are Pearson Product Moment.

RESULTS

Consumption of fecal sacs

During the 6373 min of observation, tree swallow parents made 1455 visits to their nests and carried away 170 of the 334 fecal sacs produced. In the 13,184 min we observed

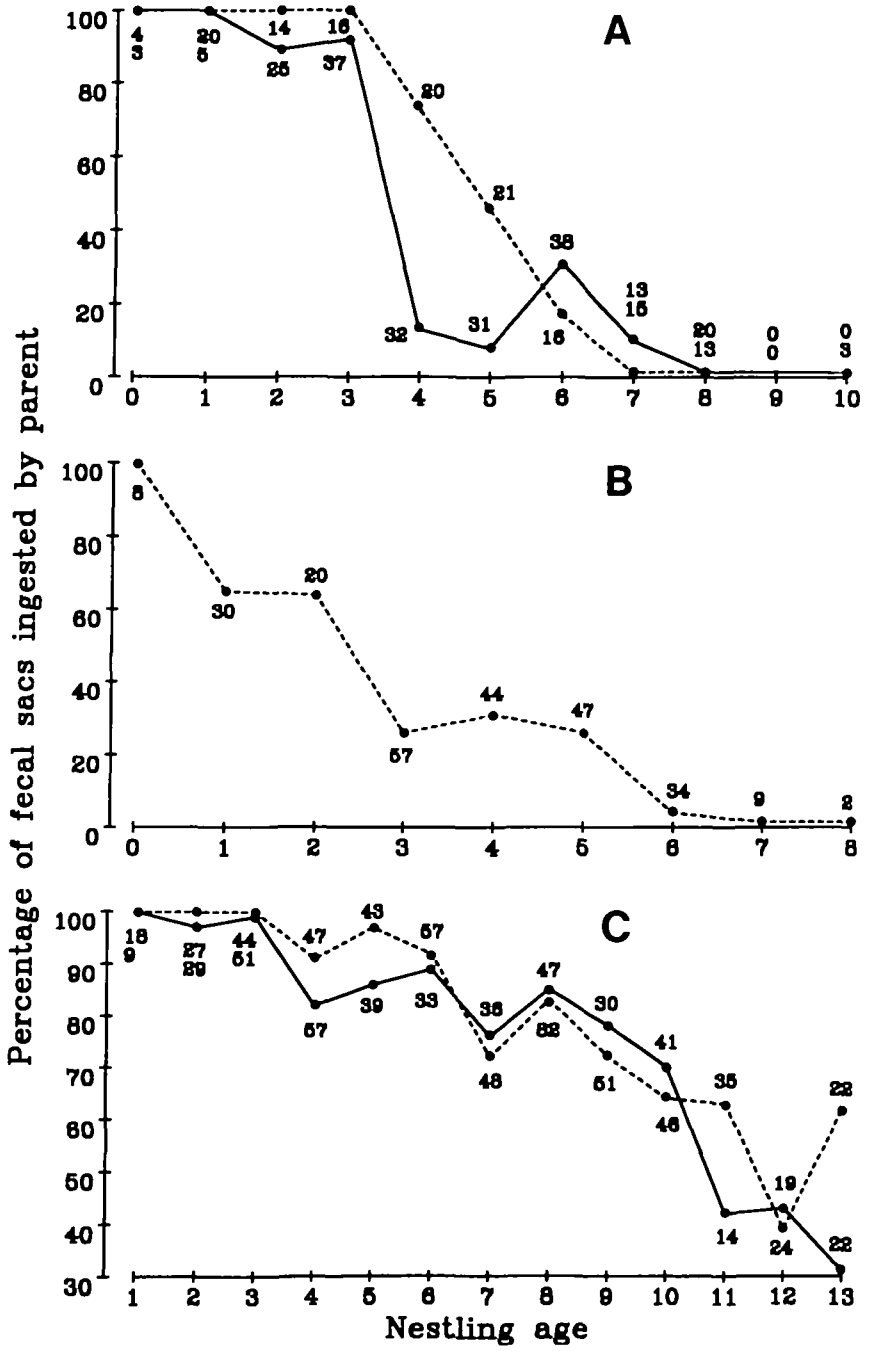

Figure 1
The percentage of fecal sacs eaten by parents relative to nestling age for (A) male (solid line) and female (broken line) tree swallows, (B) female red-winged blackbirds, and (C) male (solid line) and female (broken line) American robins. Numbers indicate the number of observations of fecal sac disposal. Where points are close, the sample size for females is above that for males.

American robins, parents visited the nest on 1251 occasions and carried away 181 of the 963 fecal sacs produced. In both species, male and female parents both contributed substantially to these observations (see below). In contrast, during the 5687 min we observed red-winged blackbird nests, male parents accounted for only 34 of the 691 visits. Thus, we exclude male red-winged blackbirds from our analyses. Females carried 166 of the 261 fecal sacs from the nest.

Male and female tree swallows both ate most of the fecal sacs they handled for the first few days of the nestling period and then rapidly switched to carrying fecal sacs from the nest exclusively by day 8 (Figure 1A). Males switched to carrying sooner than females and overall carried a higher proportion of the sacs they handled based on the mean values in Figure 1A ($\chi^2 = 17.79$, $p < .001$).

Female red-winged blackbirds showed a gradual decline in fecal sac consumption from the time the nestlings hatched until they were 7 days old (Figure 1B). This is somewhat in contrast to the rapid switch from eating to carrying shown by tree swallows, although both species exclusively carried fecal sacs after their nestlings were 8 days old.

Both male and female robins also ate fewer fecal sacs as their nestlings got older (Figure 1C). However, unlike the other two species, robins continued eating a substantial proportion of fecal sacs throughout the nestling period. From the mean values in Figure 1C, male and female robins did not differ in the overall proportion of fecal sacs eaten ($\chi^2 = 1.16$, $p = .28$).

Fecal sac analysis

Contrary to the assumption of the good food hypothesis, the energy density (j/mg dry weight) of tree swallow fecal sacs did not change significantly as nestlings aged ($r = -.30$, $p = .076$, $N = 36$, Figure 2A). Nor did the percentage by weight of the sacs that was incombustible change significantly with nestling age ($r = -.32$, $p = .58$, $N = 36$, Figure 2B). However, older nestlings produced larger fecal sacs, as indicated by the significant increase in dry weight of fecal sacs with nestling age ($r = .79$, $p < .001$, $N = 52$, Figure 2C). As a consequence, the mean proportion of fecal sacs eaten by both male and female tree swallows (Figure 1A) was significantly negatively correlated with mean fecal sac dry weight ($r = -.74$ and $-.87$, $p = .023$ and $.001$, $N = 9$ and 10, respectively). The mean consumption of fecal sacs by male tree swallows was not significantly correlated with the mean energy density of fecal sacs ($r = .46$, $p = .22$, $N = 9$). Curiously, the corresponding mean values for females were significantly correlated ($r = .78$, $p = .02$, $N = 9$). From Figure 1A and Figure 2, it is apparent that this is a spurious result due to the mean energy density values being slightly higher during the first half of the nestling period. Regardless, female fecal sac consumption is better correlated with fecal sac weight than with fecal sac energy density. These results support the sound economic hypothesis.

The results for female red-winged blackbirds were also more consistent with the hypothesis that fecal sacs are eaten as an economical means of disposal rather than for their

food quality. Energy density of fecal sacs was not significantly correlated with nestling age ($r = -.24$, $p = .16$, $N = 35$, Figure 3A), nor was the component of fecal sacs that was incombustible ($r = .11$, $p = .51$, $N = 35$, Figure 3B). However, older nestlings produced fecal sacs of higher dry weights ($r = .77$, $p < .001$, $N = 37$, Figure 3C), resulting in a significant negative correlation between mean fecal sac consumption (Figure 1B) and mean dry weight ($r = -.89$, $p < .005$, $N = 9$). There was no significant correlation between the percentage of fecal sacs consumed and their mean energy density ($r = .25$, $p = .53$, $N = 9$).

The results for robins were also consistent with our alternative hypothesis. The energy density of robin fecal sacs was not significantly correlated with nestling age ($r = -.10$, $p = .53$, $N = 44$, Figure 4A) nor was the incombustible component ($r = .01$, $p = .93$, $N = 44$, Figure 4B). Older robin nestlings produced heavier fecal sacs ($r = .64$, $p < .001$, $N = 45$, Figure 4C), resulting in a significant negative correlation between mean female robin consumption of fecal sacs and mean fecal sac dry weight ($r = -.70$, $p = .02$, $N = 10$). The correlation for male robins was not significant ($r = -.56$, $p = .08$, $N = 10$). The correlations between mean fecal sac consumption (Figure 1C) and mean energy density of fecal sacs were not significant for either male or female robins ($r = -.002$ and $.11$, $p = .99$ and $.75$, respectively, both Ns = 10).

We predicted that if parents eat fecal sacs for their energy content, then, interspecifically, the species with the highest consumption of fecal sacs should also have the most nutritious fecal sacs. Our results clearly do not support that prediction. American robins ate nearly 80% of their nestlings' fecal sacs overall even though the mean energy density of their fecal sacs was only 0.6 j/mg. In contrast, tree swallows and female red-winged blackbirds ate less than 50% of their nestlings' fecal sacs overall; the fecal sacs of both species had mean energy densities of approximately 1.0 j/mg.

Consequences of consumption

Our results thus far indicate that parents do not eat fecal sacs for nutritional reasons. Therefore, we looked for evidence of changes in parental behavior when they ate fecal sacs. We mentioned earlier that parents that carried fecal sacs from the nest invariably left the nest as soon as they had the fecal sac in their bill. Parents that ate fecal sacs did so at the nest and often remained at the nest after eating the fecal sac. To examine this pattern in more detail we assessed the time parents spent at the nest on visits when they ate a fecal sac,

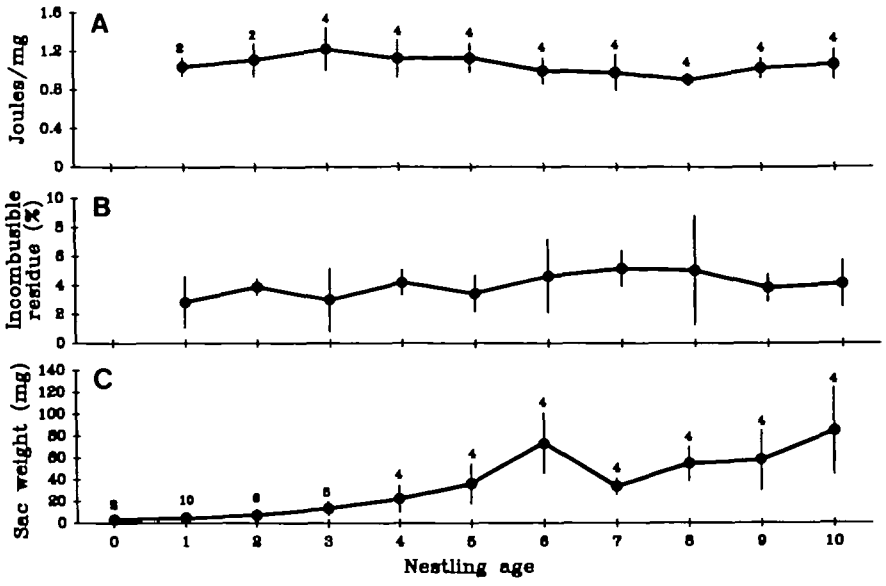

Figure 2
Variation in tree swallow fecal sac (A) energy density (j/mg), (B) percentage incombustible residue, and (C) weight (mg) relative to nestling age.

relative to nestling age, for male and female tree swallows, female red-winged blackbirds, and male and female robins (Figure 5). The time that parents spent at the nest declined significantly with nestling age for both male and female tree swallows ($r = -.27$ and $-.36$, $p = .015$ and $.002$, $N = 79$ and 76, respectively) and female robins ($r = -.39$, $p < .0005$, $N = 300$), but not for female red-winged blackbirds ($r = -.21$, $p = .09$, $N = 68$) or male robins ($r = -.02$, $p = .38$, $N = 232$).

One advantage to remaining at the nest is being able to brood the young. The greater consumption of fecal sacs from younger nestlings is consistent with the greater need to brood young nestlings. Older nestlings may also require a higher rate of food delivery, thereby decreasing the time spent at the nest. However, since only females brood nestlings, the need to brood does not explain the consumption patterns we observed for male tree

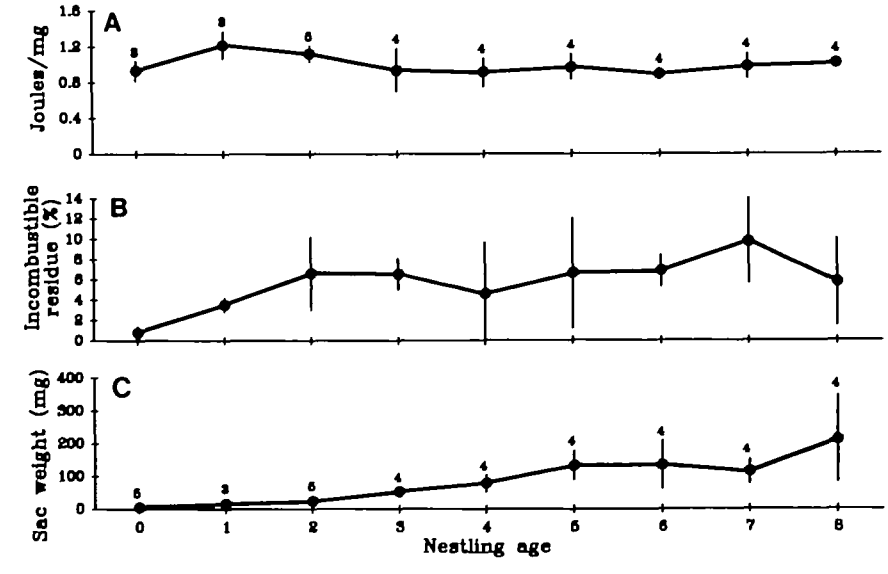

Figure 3
Variation in red-winged blackbird fecal sac (A) energy density (j/mg), (B) percentage incombustible residue, and (C) weight (mg) relative to nestling age.

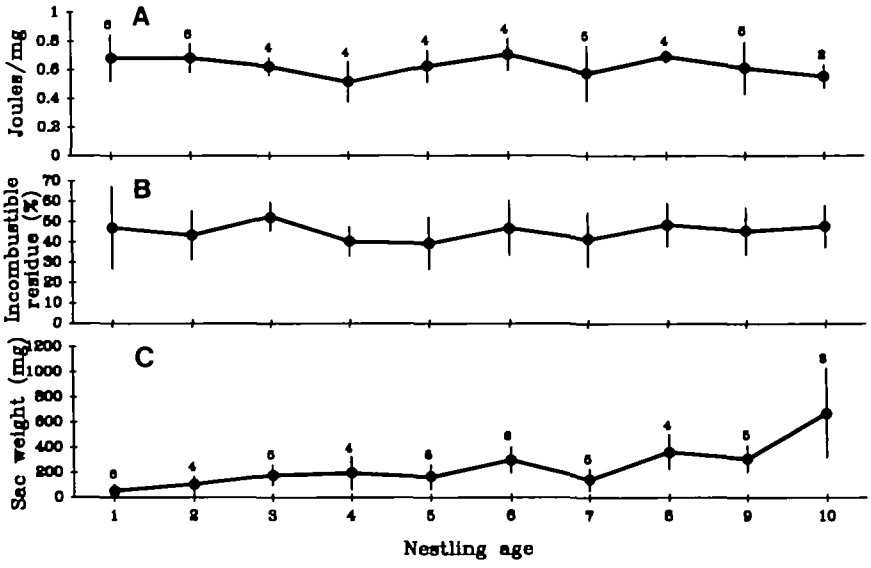

Figure 4
Variation in American robin fecal sac (A) energy density (j/mg), (B) percentage incombustible residue, and (C) weight (mg) relative to nestling age.

swallows. Brooding is also more important at cooler temperatures. If eating fecal sacs serves in part to facilitate brooding, then the females' but not the males' fecal sac consumption rate should be negatively correlated with temperature. Air temperature was not correlated with the percentage of fecal sacs eaten by male tree swallows ($r = .08$, $p = .71$, $N = 22$), female tree swallows ($r = .03$, $p = .88$, $N = 25$), or female red-winged blackbirds ($r = -.28$, $p = .17$, $N = 26$). However, consistent with the prediction, female robins ate a higher percentage of fecal sacs at cooler temperatures ($r = -.25$, $p = .004$, $N = 129$), whereas males did not ($r = .05$, $p = .96$, $N = 133$). Thus we have evidence that parents tend to eat fecal sacs when staying at the nest, and that this behavior may facilitate other aspects of parental care such as brooding.

DISCUSSION

Our observations for all three species were consistent with the previously reported pattern (Blair and Tucker, 1941; Conder, 1948; Gluck, 1988; Herrick, 1900) of parents decreasing the proportion of their nestlings' fecal sacs that they eat as the nestlings get older. Our results did not support the hypothesis that this pattern is a consequence of a decline in energy content of fecal sacs with nestling age. The energy density of fecal sacs of all three species remained relatively constant. Thus, parents were not eating fecal sacs when they had a higher relative energy content. Furthermore, because fecal sacs became larger with nestling age, parents were actually eating fewer fecal sacs as the absolute energy content of the fecal sacs increased.

The alternative hypothesis that we proposed, that parents eat fecal sacs as an economical alternative to carrying them from the nest, better explained our observations. Parents ate fecal sacs when they were small. Larger fecal sacs would occupy a greater proportion of the digestive tract and thus are presumably more of a burden on the parents' digestive system. Parents that ate fecal sacs tended to remain longer at the nest, particularly when nestlings were young, and female robins ate more fecal sacs in cooler weather, when the need to brood nestlings was presumably higher.

Although the general patterns for all three species we studied were consistent with our alternative hypothesis, there were several contrasts in the specific patterns we observed. Female red-winged blackbirds began steadily reducing fecal sac consumption from the day their nestlings hatched, whereas tree swallow parents showed a step-like decrease. Neither species ate any fecal sacs after their nestlings were 8 days old. However, robin parents continued eating a substantial proportion of fecal sacs throughout the nestling period. Two factors that may have contributed to these differences are the cost of disposing of fecal sacs carried from the nest and the cost of eating fecal sacs. Weatherhead (1984) showed that tree swallows nesting over water drop their fecal sacs much closer to their nests than do those nesting over land, presumably due to the superior dispersal properties of water. All the red-winged blackbird nests we observed were in marshes, so female red-winged blackbirds presumably dropped fecal sacs in water when they carried them from the nest. Most of the tree swallow nests we studied were either over water or near water, with two being located in upland habitat. All of the robin nests were located in upland habitat. If all birds tend to carry fecal sacs farther from the nest when dropping them over land than over water, then, on average, the cost of carrying fecal sacs in our study was highest for robins and lowest for red-winged blackbirds. The absence of male assistance (and thus disposal of fecal sacs) would also have increased the cost of eating fecal sacs for female red-winged blackbirds and may have contributed to the quick decline in consumption that we observed.

We have assumed that a cost to parents of eating fecal sacs is reduced digestive efficiency. To actually demonstrate a cost would require a controlled feeding experiment. Nonetheless, the assumption seems reasonable. Parents feeding nestlings have high energy demands and must process food quickly to meet those demands. Even if nestling feces are not toxic, they do contain indigestible material. The presence of such material probably decreases the parents' digestive efficiency by re-

ducing the surface area available for absorption of nutrients for a prolonged period. It is possible that eating large fecal sacs could adversely affect digestive efficiency, but that the same volume of small fecal sacs could be processed, thus leaving the system sooner. The mean fecal sac dry weight for robins as a percentage of mean adult weight is 0.24% compared to 0.16% for tree swallows and 0.24% for female red-winged blackbirds. Thus, differences in the relative size of fecal sacs do not account for the differences between species we observed in consumption patterns. Nevertheless, the capacity of the parents' digestive systems may constrain their ability to consume the feces of older nestlings (i.e., the total volume of fecal sacs might be too large for them to manage).

Thus far, the variation in fecal sac consumption that we have discussed has not been extreme (i.e., all species carry some fecal sacs and eat some fecal sacs). However, European starling (*Sturnus vulgaris*) parents apparently never eat their nestlings' feces (Blair and Tucker, 1941), whereas white-crowned sparrow parents eat all of their nestlings' feces (Morton, 1979). Thus, just with the small number of species studied to date, the interspecific variation in fecal sac disposal by parents spans the entire range of possibilities. In an attempt to explain some of this variation we discovered a curious anomaly in the energy density values reported for different species. In two studies (Gluck, 1988; Morton, 1979), the lowest daily mean energy densities of fecal sacs reported were approximately 15 j/mg. In contrast, our study and Westerterp's (1973) both produced minimum daily means of approximately 1 j/mg, more than an order of magnitude lower. This difference is not due to the specific method of calorimetry employed because Gluck used the same method as we did (microbomb calorimetry). Nonetheless, we feel that methodological problems are responsible for the huge differences in values because it is unlikely that different passerine species could exhibit such dramatic variation in digestive efficiency.

While it remains for future studies to solve the mystery of the interspecific variation in absolute energy densities of fecal sacs, we can reach some conclusions now from the relative change in energy density and the patterns of parental disposal behavior. Within species, it is clear that what the parents gain from eating a fecal sac has little influence on their decision of whether to eat it. Rather, the cost of eating the sac relative to the cost of carrying it appears to determine parental behavior. Because these costs will vary with ecological circumstances, both inter- and intraspecifically, fecal sac disposal behavior will be an excellent model for studying economic decision making by birds.

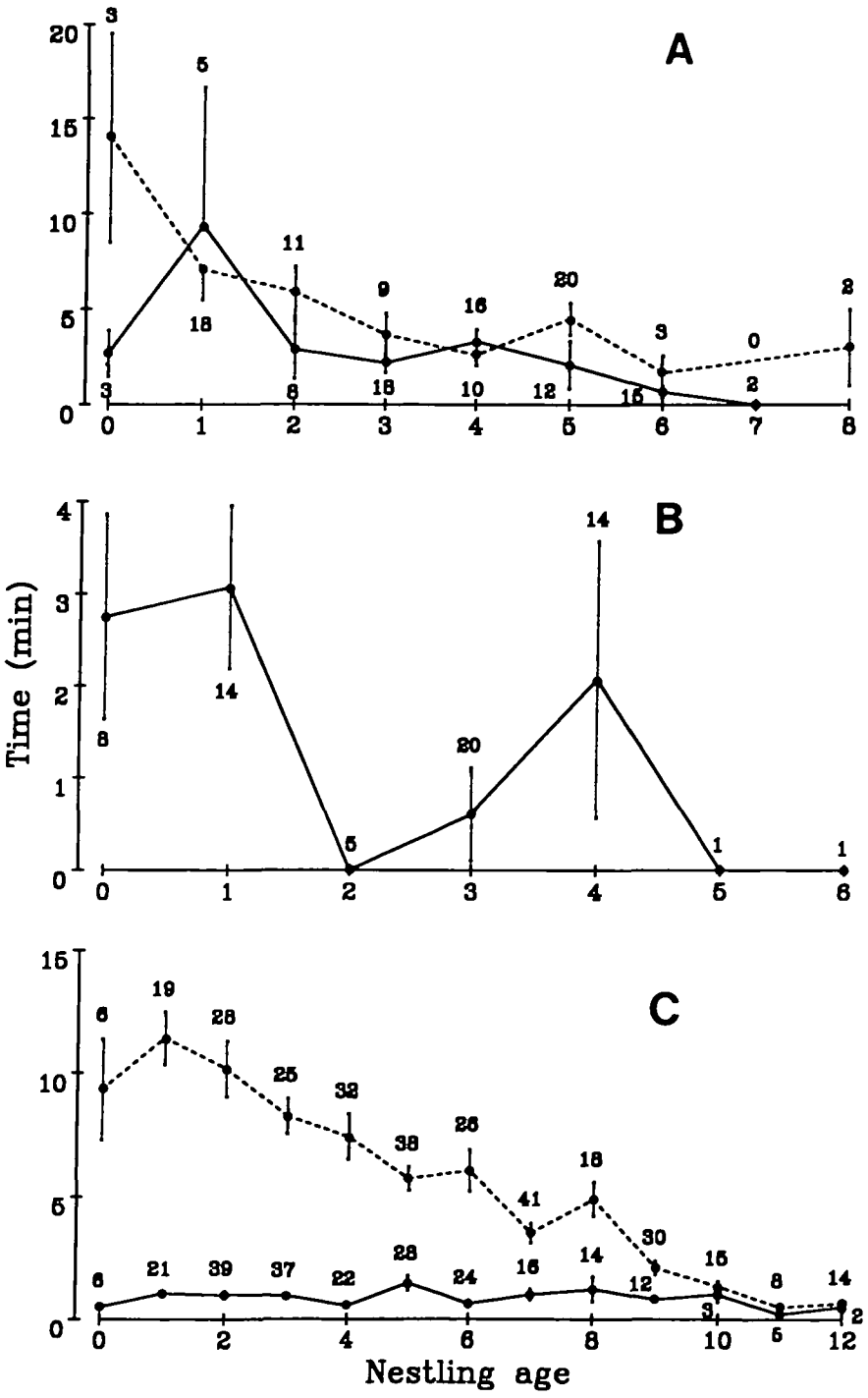

Figure 5
Mean (±0.5 SE) time spent at the nest after eating a fecal sac for (A) male (solid line) and female (broken line) tree swallows and (B) female red-winged blackbirds, and (C) the mean duration of nest visits when a fecal sac was eaten (see Methods) for male (solid line) and female (broken line) American robins. Numbers indicate sample sizes.

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