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A TEST OF WHETHER ECONOMY OR NUTRITION DETERMINES FECAL SAC INGESTION IN NESTING CORVIDS[1]

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Abstract. Parent birds of many species eat the fecal sacs produced by their nestlings. Two hypotheses have been proposed to explain why the parents ingest, rather than simply remove the sacs. (1) The parental nutrition hypothesis proposes that the parent benefits energetically or nutritionally from ingesting the sacs (Morton 1979, Glück 1988); and (2) the economic disposal hypothesis postulates that parents incur some costs from eating waste products, but the cost of eating them is less than the benefits gained from being allowed to remain at the nest (Hurd et al. 1991). Behavioral data on nesting Florida Scrub Jays (*Aphelocoma c. coerulescens*) and American Crows (*Corvus brachyrhynchos*) support the parental nutrition, and not the economic disposal hypothesis. In both species, when two parents were present at the production of fecal sacs, the most nutritionally stressed parent, the female, ate significantly more sacs than her mate. On occasions where one adult left the nest immediately after fecal sac production and one remained, the departing adult was not more likely to dispose of the sac in either species. In neither species was a departing adult more likely to carry off a fecal sac than eat it.

Key words: Corvidae; fecal sac; nest maintenance; American Crow; Corvus brachyrhynchos; *Florida Scrub Jay;* Aphelocoma coerulescens.

INTRODUCTION

In passerines, ingestion of nestling fecal sacs by parent birds is a widespread occurrence (Blair and Tucker 1941, Tucker 1941). The removal of feces of nesting birds provides sanitation and lessens the attractiveness of the nest to predators (Welty and Baptista 1988), but the presence of a mucosal sac around the feces allows parents the option of carrying them away. One explanation for ingestion rather than removal and dropping of feces, that I call the "parental nutrition hypothesis," postulates that parents benefit energetically or nutritionally from ingesting fecal sacs because the inefficient digestive processes of the nestlings leave significant amounts of food behind (Morton 1979, Glück 1988). Recently Hurd et al. (1991) suggested a second explanation. This idea, which I call the "economic disposal hypothesis," postulates that rather than the parents gaining energetically, they incur some cost in eating the fecal sacs because of the waste products. Parents eat fecal sacs only because other parental activities sometimes make the benefit of eating them exceed the costs. Benefits could be savings in time and energy needed to fly away and dispose of the sacs, or in allowing the parents to perform other actions. For example, by eating a fecal sac the parent bird could then remain at the nest and brood the young without leaving them exposed.

Hurd et al. (1991) tested these two hypotheses by examining the phenomenon of a decrease in the proportion of fecal sacs ingested with increasing nestling age. The parental nutrition hypothesis explains this decrease by assuming an increase in nestling digestive efficiency and a consequent decrease in the food value of the fecal sac (Glück 1988). The economic disposal hypothesis explains the decrease by the increasing cost placed on the parents by the increasing size of the fecal sacs along with a decreasing need to remain at the nest as the nestlings grow. Hurd et al. (1991) compared the digestive efficiency of the nestlings of three passerine species with the adult fecal sac consumption rate. They found that although fecal sac consumption decreased as the young developed, no change in energy content per gram of the fecal sacs was noted, and they rejected the parental nutrition hypothesis.

Hurd et al. (1991), however, failed to consider components of nutrition other than energy. Nor did they consider the value of the food to the parent birds. That is, directly after egg laying and incubation the food value of the nestlings' feces

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may be more important than later in the nesting cycle. The female may need to replace protein and calcium after egg laying in addition to energy stores (e.g., Ricklefs 1974). Therefore, the nutritional value of the food stuffs in fecal sacs may change without any change in energy content. With this idea in mind I generated three additional ways to distinguish between the economic disposal and parental nutrition hypotheses using parental behavior.

Test No. 1. If parental condition can affect the value of fecal sac consumption, one could compare the actions of the sexes in a species with highly specialized sex roles, and therefore differing energetic and nutritional costs during reproduction. The test is to determine which sex eats the fecal sac when both parents are present at defecation. The parental nutrition hypothesis predicts that the sex for whom the food has the most value, the more-stressed sex, should eat the fecal sac. A logical extension of the economic disposal hypothesis predicts that the less-stressed sex should eat the fecal sac and deal with the waste products. Even if no great difference in nutritional status exists between the sexes, the parental nutrition hypothesis predicts that the parent that has gone the longest without foraging (e.g., the brooding female) should eat the fecal sac, while the economic disposal hypothesis predicts no difference or that the parent that fed most recently should dispose of the sac.

Test No. 2. If two birds are present at the nest at the same time and one stays and the other leaves after a nestling defecates, the two hypotheses make different predictions about which one should dispose of the fecal sac. The economic disposal theory predicts that the departing bird should always take the fecal sac away; if one bird leaves and could dispose of the sac, there is no need for the remaining bird to incur the physiological cost of consuming it. The parental nutrition hypothesis predicts no difference, or that the bird staying should eat the sac because it will be longer without food.

Test No. 3. Similarly, the two hypotheses make different predictions about what a solitary adult should do when it leaves immediately after the nestlings defecate. The parental nutrition hypothesis predicts no difference between the actions of parents staying or leaving; when the food value of the sac is high it should be eaten, when low it should be carried away. The economic disposal hypothesis predicts that a bird leaving the nest should always carry the fecal sac away unless specific disposal needs (e.g., a specialized disposal site, see Weatherhead 1988) impart too great a cost.

I tested these three predictions in nesting American Crows (*Corvus brachyrhynchos*) in central New York, and Florida Scrub Jays (*Aphelocoma coerulescens coerulescens*) in central Florida. Birds in the family Corvidae are appropriate for making these tests because, in general, although both sexes attend the young, only the female of a pair lays eggs, incubates, and broods the young (Goodwin 1975). Therefore, the female should incur the higher energetic or nutritional cost. Because the female may brood throughout much of the nestling period (e.g., *Corvus brachyrhynchos*, Kilham 1989), and the nests are open cups, both parents frequently are present at the nest at the same time and have equal opportunity to dispose of the fecal sacs. Both species have the complication of the presence of auxiliaries at the nest feeding young (see Kilham 1984, Woolfenden and Fitzpatrick 1984, Chamberlain-Auger et al. 1990, Caffrey 1992). However, the presence of extra birds at the nest does not affect the predictions made above, as in both species only the breeding female lays, incubates, and broods (Woolfenden and Fitzpatrick 1984; Kilham 1989; Caffrey, pers. comm; pers. observ.).

METHODS

I collected data on American Crows during the spring and summer of 1989, 1990, and 1991 as part of an on-going study of breeding and social behavior in urban Ithaca and suburban Tompkins County in the Finger Lakes region of central New York. Because nests in the study population are usually high in tall trees ($\bar{x}$ nest height = 18 m), nests are not easily checked, and routinely are observed from the ground. Nest watches were performed throughout the nesting cycle, usually for periods of about one hour. Observations were made from inside vehicles, using a spotting scope with a zoom lens. Over the three years I observed 40 nests containing nestlings for 84 hr (n = 97 observation periods). Although some instances of fecal sac ingestion undoubtedly were missed, crows often were obvious when they disposed of fecal sacs. After the adult ate a fecal sac, swallowing was conspicuous. When sacs were carried away, no swallowing by the adult was noted, the throat was visibly distended, and often the bill

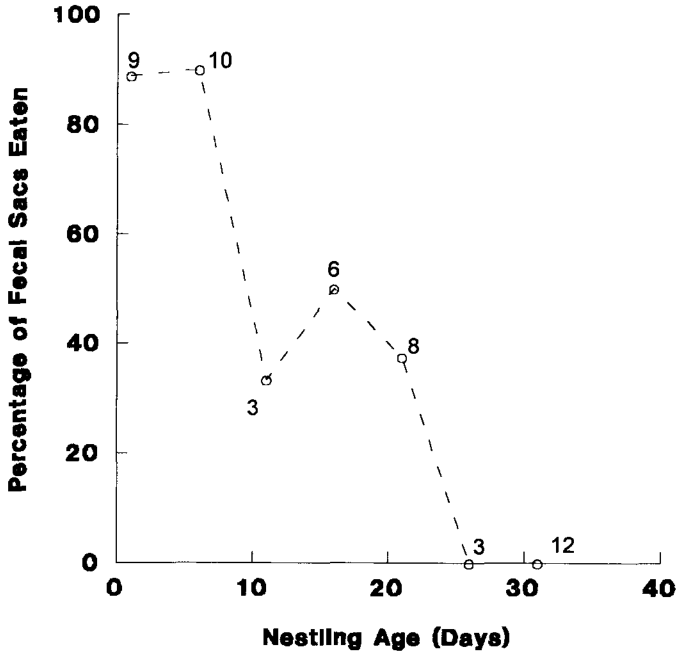

FIGURE 1. The percentage of fecal sacs produced by nestling American Crows that were consumed by attendants, relative to nestling age. Data were combined into five-day categories. Numbers near each data point represent the total number of fecal sacs observed produced at each age.

remained partly open with the white fecal sac visible.

Many auxiliary crows hatched in previous years were marked with wing tags and colored leg bands, but no breeders in the study were individually marked. The identity of unmarked crows was determined by the performance of brooding: the brooding crow was assumed to be one bird, the breeding female. Although male American Crows have been reported to brood and incubate (e.g., Bent 1946), such behavior appears unlikely (Goodwin 1975, pers. observ.), and may be traced back to the unsupported report of Bendire (1895). Other studies of American Crows have found that only the female incubates and broods (Good 1952; Kilham 1989; Caffrey, pers. comm.), as is also true for the closely related Northwestern Crow *Corvus caurinus* (Butler et al. 1984).

I collected data on Florida Scrub Jays during the summer of 1984 as part of a study of the provisioning of fledglings (McGowan and Woolfenden 1990). I watch 11 nests containing nestlings for 57 hr ($n = 29$ observation periods). Mean nest height in this population is 1 m and the jays were tame (see Woolfenden and Fitzpatrick 1984), allowing excellent observation with a spotting scope from within 30 m. Disposal of fecal sacs, whether by ingestion or removal, was obvious and easily recorded. All jays in the study population were individually marked, and their age, sex, and breeding status were known.

For both species any bias in detection of fecal sac disposal related to nestling age was investigated by using the log likelihood ratio test (Sokal and Rohlf 1981) to compare the occurrences of observed disposal with the distribution of total feeding events. Deviation from equity of disposal for each of the three hypotheses was detected with binomial tests (Sokal and Rohlf 1981).

RESULTS

AMERICAN CROW

During the 5,062 min of nest observation, I observed 366 feeding visits and 54 instances of fecal sac disposal. The adult crows ate 24 fecal sacs, carried away 23, and attempted to dispose of, but failed to catch four that fell from the nest. All adult crows alone at the nest when fecal sacs were produced disposed of the sacs; none ignored the sacs and let them drop. Observations were grouped in seven five-day blocks for analysis: 1–

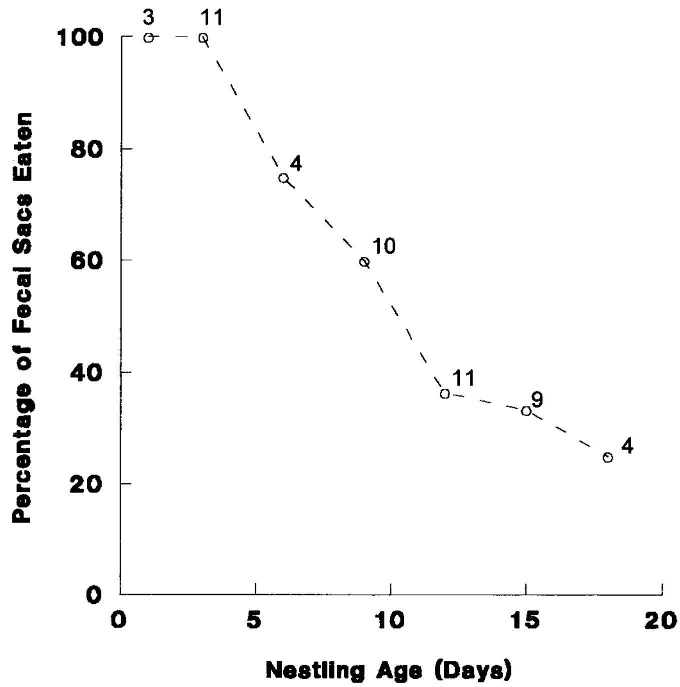

FIGURE 2. The percentage of fecal sacs produced by nestling Florida Scrub Jays that were consumed by attendants, relative to nestling age. Data were combined into three-day categories. Numbers near each data point represent the total number of fecal sacs observed produced at each age.

5 days old, 6–10, 11–15, 16–20, 21–25, 26–30, 31–35. Detection of fecal sac disposal was not biased by nestling age: observed disposals were equally distributed throughout the 35+ day nestling period ($G = 4.116$, df = 6, $P > 0.50$). Fecal sac ingestion by adults declined as the nestling period progressed (Fig. 1).

On 15 occasions when the female was brooding, another adult arrived to feed the nestlings and both stayed for the production of a fecal sac. Of these 15 fecal sacs, 10 were eaten and five removed. Of the ten that were eaten, the brooding female ate all ten (binomial test, $P = 0.001$). Adults other than the breeding female were observed consuming fecal sacs on other occasions.

On 15 occasions when two crows were present at defecation, one individual stayed at the nest (for at least 1 min) and the other left immediately (in less than 15 sec). Of these 15 fecal sacs, the departing crow disposed of seven and the remaining crow disposed of eight (binomial test, $P = 0.50$).

Of the 25 occasions when the crow receiving the fecal sac left the nest immediately, the fecal sac was removed 21 times and eaten four times. If only those 14 cases occurring before day 25 (when some sacs are eaten, Fig. 1) are considered, 10 were removed and four eaten (binomial test, $P = 0.09$).

FLORIDA SCRUB JAY

During the 3,440 min of nest observation, I observed 380 feeding visits and 52 instances of fecal sac disposal. The adult jays ate 31 sacs and removed 21. Female breeders dealt with 25 sacs (18 eaten, 7 removed), male breeders 24 (11 eaten, 13 removed), and helpers 3 (2 eaten, 1 removed). Observations were grouped into three-day categories for analysis. Observed disposals were equally distributed throughout the 18-day nestling period ($G = 4.092$, df = 6, $P > 0.50$), with one disposal observed of a sac from a 20 day-old fledgling. As in the crows, fecal sac ingestion by adults declined as the nestling period progressed (Fig. 2).

On 16 occasions when the female was brooding, another adult arrived to feed the nestlings and both stayed for the production of the fecal sac. Of these 16 sacs, 13 were eaten and three removed. Of the 13 that were eaten, the brooding female ate 12 and the male breeder one (binomial test, $P = 0.002$). The one occasion when the male ate the sac, two were produced and the female ate the first at the same time the male ate the second.

On 12 occasions when two adult jays were present at defecation, one individual stayed at the nest and the other left immediately. Of these 12 sacs, the departing jay disposed of four and the remaining jay disposed of eight (binomial test, $P = 0.19$).

Of the 36 occasions when the jay taking the fecal sac left the nest immediately, the fecal sac was removed 20 times and eaten 16 times (binomial test, $P = 0.31$).

DISCUSSION

The results presented here support the parental nutrition hypothesis and not the economic disposal hypothesis for all three tests. In both species when two birds were present at the nest, the presumed more nutritionally-stressed individual, the breeding female, was more likely to consume the fecal sac than any other bird. In Florida Scrub Jays the total number of fecal sacs disposed of by breeding males was equal to that disposed of by breeding females. When both were together at the production of a sac, however, the female was far more likely to dispose of the sac, usually by eating it. For both species, when two birds were present, birds leaving the nest immediately were not more likely to dispose of fecal sacs than those remaining. In neither species were birds leaving the nest immediately after production of the fecal sac more likely to carry the sac away than eat it. Disposal of fecal sacs by birds leaving the nest immediately could still be more costly than ingestion if they were transported some distance away from the nest, as reported by Weatherhead (1984). However, crows in this study were observed disposing of fecal sacs within the vicinity of the nest, by placing them on branches within 50 m of the nest tree; foraging areas were often much farther away. Florida Scrub Jays routinely deposited fecal sacs in trees near the nest shrub, closer to the nest than the major foraging areas. Neither species disposed of them in water, which might impose a specific route of travel and therefore a potentially greater cost (Weatherhead 1988).

The prediction of the economic disposal hypothesis for test #3, that birds leaving the nest immediately should eat no sacs, is not supported by data presented by Hurd et al. (1991). Their Figure 5C (p. 75) shows that male American Robins (*Turdus migratorius*) rarely stayed at the nest over one minute when a fecal sac was eaten, yet they frequently ingested fecal sacs. If males left the nest more rapidly than females, whose nest visits averaged significantly longer, they should have been more likely than females to carry away fecal sacs throughout the nestling period. However, the proportion of fecal sacs consumed by the sexes appears nearly identical (p. 72, Fig. 1C).

Hurd et al. (1991) found no increase in energy content per unit weight of fecal sacs over time, and therefore rejected the hypothesis of increasing digestive efficiency to explain the decrease in fecal sac consumption by parents as nestlings aged. They postulated that the parents switch from eating to dumping sacs because the increasing size of the sacs take up more gut volume and become too costly to eat. However, the relationship of feces consumed and fecal sac size, as represented by mass, they report does not obviously support their contentions. Female Tree Swallows eat approximately 50% of the fecal sacs on day 5, but drop to 0% by day 7 (p. 72, Fig. 1A), yet the masses of the sacs on the two days are identical (p. 73, Fig. 2C). For male Tree Swallows, a barely detectable increase in sac mass from day 3 to day 4 (p. 73, Fig. 2C) corresponds to a drop in male consumption from about 90% to about 12% (p. 72, Fig. 1A). If mass is an important factor influencing the decision to eat or remove fecal sacs, the exact nature of the relationship is not obvious.

The use in some studies (e.g., Morton 1979, Glück 1988, Hurd et al. 1991) of simple energy density and incombustible residue to assess the nutritional value of feces may be inappropriate. Energy values of biological materials are not related to their digestibilities. Birds do not digest the energy-dense materials from their diets and leave the energy-light materials necessarily. Waxes, cellulose, chitin and similar sugar-based materials of the food of birds may be indigestible and useless for the bird, but contain substantial amounts of energy, as much as sugars. All these substances will combust in a bomb calorimeter and contribute to the measured energy density of feces, even though they would not be available for an adult ingesting them. The incombustible residue (ash) would be expected to be a small part of the feces. As stated by Robbins (1983, p.

9), "Since the degree of dietary energy use [of high-energy compounds] may vary from 0 to 100% depending on the completeness of digestion and oxidation, gross energies must be further evaluated to understand animal energetics." Available energy in fecal sacs could in fact be changing significantly over the nestling period, but could be masked by the large indigestible component. This possibility might be especially likely in the feces of insectivorous birds where indigestible chitin can be a major part of the fecal matter. A more appropriate measure of available energy would be the examination of total metabolizable energy, with the values for the indigestible portion subtracted out (e.g., Stiven 1961). Perhaps the use of a different technique would clear up the more than ten-fold discrepancy in energy density values of fecal sacs found by Morton (1979), Glück (1988), and Hurd et al. (1991).

In some species the cost of disposal may be an important factor influencing the behavior of parent birds, although the costs of disposal probably differ greatly among species. An economic approach to fecal sac disposal should be useful, but all parts of the economic equation should be considered. Such an approach would consider nutrients available from the fecal sacs and the nutritional needs of the parents as well as energy. Ingestion of fecal sacs could be important for parent birds as a source of protein, nitrogen, and calcium. Also, water may be an important commodity for the parents in some desert birds (Calder 1968). Van Riper (1987) observed that Common Amakihi (*Hemignathus virens*) parents ate most fecal sacs of young nestlings, but that as the nestlings got older the parents flayed the sacs against branches and ate only the mucosal coverings. This observation makes sense only if the contents of the sac, especially the proteins of the sac itself, were food in which the parents were interested. The fact that the parental behavior changed from ingesting all of the sacs to ingesting only the coverings is consistent with the idea that digestible content of the sacs change with nestling development.

The consumption of fecal sacs by parent birds may be a more complex problem than it first appears. Certainly the rapid change from eating to removing sacs in Tree Swallows over the course of only a couple of days (Hurd et al. 1991) has yet to be explained by either hypothesis considered here. More work is needed on the ontogeny of digestion and the nutritional content of the feces, as well as on parental nutrient balance and digestive efficiencies to understand this phenomenon clearly. Other factors may also be involved that have not yet been considered. Intestinal parasite presence could influence the decrease in parental likelihood of ingestion, and might partially explain the step-like decline noted in several studies (e.g., Hurd et al. 1991, p. 72, Fig 1A). Parents might eat feces until the length of the prepatent stage of the most prevalent parasites. That is, after a parasite has had time to mature and begin to shed eggs through the feces of the host, the cost of ingesting fecal sacs of the host would rise. If fecal sacs are safe to ingest up to that point, but not afterwards, then one could predict the point of abrupt decline in consumption rates by knowing the prepatent period of the most important intestinal parasites. It also is possible that parent birds use the contents of fecal sacs to assess the physiological condition of nestlings. Perhaps they can detect developmental abnormalities, congenital deficiencies, or the presence of parasites by chemical cues in the feces. Such information could influence decisions about brood reduction, whether to actively reduce the brood or not, and whom to discard. Information from waste products could also influence foraging choices by alerting the parents to differing developmental needs of the young for micro-nutrients. In this regard, fecal sacs are fertile ground for further investigations.

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