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FECAL SAC INGESTION IN THE MOUNTAIN WHITE-CROWNED SPARROW

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Nestling passerines void their urine and feces encapsulated within a whitish mucosal structure called the fecal sac. Parent birds in most species dispose of sacs by carrying them away or swallowing them (Van Tyne and Berger 1959). Despite interspecific and individual differences in disposal techniques and propensity to ingest sacs, a general pattern can be discerned. In data gathered on more than 70 European species, Blair and Tucker (1941) found that sacs produced during the first days after hatching tend to be swallowed. As nestlings and their sacs become larger, parents swallow fewer sacs and carry away and drop more. Finally, during the last days of nest occupancy, some sacs are not handled by adults at all but are simply deposited by nestlings on the rim of the nest. These stages and their transition periods are illustrated in an exemplary study on the European Goldfinch (*Carduelis carduelis*; Conder 1948).

The value of sac disposal behavior is thought to lie in the maintenance of a clean nest; contamination of the young, their food, or the brooding parent is prevented. It may also make the nest site less conspicuous to predators (Blair and Tucker 1941).

When swallowing is the primary disposal technique, a considerable volume of sac material is ingested daily by the parents. This has led to speculation concerning the possible nutritive value of sacs (Herrick 1900, Tucker 1941), and their contribution to maintenance of water balance (Calder 1968). The composition of fecal sacs has not been examined so their importance as an energy source to adults is unknown.

Fecal sacs are usually swallowed throughout the nestling period by Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*; Morton, Orejuela and Budd 1972). Herein I report on sac composition from nestlings of this sparrow and upon the possible contribution of ingested sacs to daily water and energy requirements of parent birds.

METHODS

The fieldwork was conducted on breeding grounds of *Z. l. oriantha*: subalpine meadows in the upper regions of Lee Vining Canyon near Tioga Pass and Saddlebag Lake in the central Sierra Nevada of California.

Observations of events at the nest were made, with the aid of binoculars, from concealment within shrubbery or a blind.

Fecal sacs were collected from nestlings of known age from 24 nests in 1973 and 18 in 1976. Sacs were obtained when nestlings voided while being handled or by application of gentle pressure to the abdomen of those with sacs clearly visible through the skin. Specimens were placed immediately in capped vials, weighed later in the day to the nearest 0.2 mg on a torsion balance, sealed in vials, and kept frozen until analyzed in the laboratory.

Mean sac weight is used in this paper as an indicator of size. Due to the methods of collection, this may underestimate substantially the mass of fecal material regularly produced by undisturbed nestlings, especially the older ones. At about Day 4 nestlings begin producing sacs reflexly when handled (Morton, Orejuela and Budd 1972) and fecal specimens collected under such circumstances or by application of abdominal pressure may be smaller than normal. All specimens used in assays, however, were encapsulated in mucus.

Water content of sacs was determined by drying to constant weight in an oven at 60°C. Caloric content was determined by combustion of the dry, homogenized material in a microbomb adiabatic calorimeter. Ash content was the material remaining in the calorimetry thimble following combustion. Fat content of dried sacs was measured by soxhlet extraction for 24 h using petroleum ether as solvent. Carbohydrate content of dried sacs was determined spectrophotometrically using glucose standards (Hodge and Hofreiter 1962). Protein content of dried sacs was also determined spectrophotometrically using bovine serum albumin as a standard (Lowry et al. 1951). To remove ammonium ion as a contaminant, pulverized sac material was dialyzed for 24 h against three changes of 0.5 M sodium hydroxide in phosphate buffer (pH 7.4) stirred constantly at 5°C. This assay measures total water soluble protein but does not distinguish individual protein species.

RESULTS

RATE OF SAC PRODUCTION AND CONSUMPTION

Nestling sparrows began producing fecal sacs within a few hours after hatching. Those produced on the first day (Day 0) averaged 56.3 mg (range 33 to 80 mg, Table 1). They increased in size with age and averaged about 2 to 3% of body weight throughout the nestling period (Table 1).

As soon as adults obtained the sacs, they swallowed them at the nest or, occasionally, at a nearby perch. Sacs were not regurgitated, nor were there attempts to feed them to nestlings.

To determine how many sacs were con-

TABLE 1. Fecal sac weights of nestling *Zonotrichia leucophrys oriantha* (mg).

	Nestling age (days)									
	0	1	2	3	4	5	6	7	8	9
Mean	56.3	92.7	154.0	293.8	309.9	420.2	475.8	491.3	508.7	451.9
SD	15.4	32.3	35.2	94.7	67.6	110.7	78.6	148.1	224.6	184.9
N	15	18	21	19	14	22	16	22	11	7
Range	33–80	55–164	104–221	172–450	218–453	246–630	254–821	318–900	280–985	331–850
Mean sac weight as percent of body weight	2.1	2.2	2.4	3.2	2.5	2.6	2.1	2.5	2.5	2.2

sumed per day by parent birds throughout the nestling period, my assistants and I observed behavior at the nest for a total of 205 h. Three to seven observation periods, the briefest being 60 min, were made on nestlings of every age until fledging, which occurs on or about Day 9.

The mean number of sacs produced per day by a brood of four ranged from a low of 30.0 on Days 0 and 9 to a high of 67.6 on Day 4 (Table 2). This rate was determined by multiplying the number of sacs produced per hour by the number of hours each day that nestlings were fed. The feeding period increases with nestling age (Table 2) because females cease brooding earlier in the morning as chicks achieve thermoregulatory independence (Morton and Carey 1971). Data are presented for a brood of four because this is the modal size in *Z. l. oriantha* (Morton, Horstmann and Osborn 1972).

The rate of sac production increased with age until Day 4 and decreased thereafter. Decreased rate of sac formation by older nestlings has been noted in several passerines (Nice 1943, Conder 1948) and has been suggested to be related to digestive efficiency (Steinfatt 1938). I feel that other factors, having to do with sociality at the nest, may be involved in this trend. For example, on Day 4 or 5 *oriantha* nestlings open their eyes for the first time, begin cueing visually on their parents, respond to intruders by crouching low in the nest and, when handled, make alarm calls, gape and defecate (Morton, Orejuela and Budd 1972). Their alertness and interactions with parent birds increase thereafter. At the same time adults with older nestlings seem to become more aggressive when an observer is present and tend to interrupt food gathering while performing prolonged bouts of alarm "chipping." These observations indicate that rates of feeding and sac formation may be difficult to quantify accurately in older nestlings.

Total mass of sac material produced per day (obtained from the product of number produced per day and mean weight) was only

TABLE 2. Rate of fecal sac production by a brood of four *Z. l. oriantha* and rate of sac consumption by parent birds.

	Nestling age (days)									
	0	1	2	3	4	5	6	7	8	9
Mean number of sacs produced per hour	2.5	3.2	3.8	4.3	5.2	4.0	3.3	3.3	2.4	2.0
Hours of feeding per day	12	12	12	12	13	14	14.5	15	15	15
Sacs produced per day	30.0	38.4	45.6	51.6	67.6	56.0	47.8	49.5	36.0	30.0
Weight of sacs produced per day (g)	1.69	3.56	7.02	15.16	20.95	23.54	22.74	24.32	18.31	13.56
Sacs consumed by female per day (g)	1.35	2.39	4.29	7.75	11.44	10.56	12.14	13.69	9.66	4.8
Sacs consumed by male per day (g)	0.34	1.17	2.73	7.41	9.51	12.96	10.60	10.63	8.64	4.72

TABLE 3. Water content of fecal sacs of nestling *Z. l. oriantha* collected in 1973 and 1976 seasons and water ingested from sacs by parent birds.

	Nestling age (days)									
	0	1	2	3	4	5	6	7	8	9
Water content of sacs (%)										
1973	82.2	79.7	78.4	77.8	75.7	73.4	74.5	73.1	71.3	74.4
1976	84.6	75.7	78.8	79.8	77.3	76.1	78.5	76.1	78.5	74.3
Mean	83.4	77.7	78.6	78.8	76.5	74.8	76.5	74.6	74.9	74.4
Water ingested from sacs per day (g)										
Female	1.1	1.9	3.4	6.1	8.8	7.9	9.3	10.2	7.2	6.6
Male	0.3	0.9	2.2	5.8	7.3	9.7	8.1	7.9	6.5	3.5

1.69 g on Day 0 but was more than 20 g by Day 4 (Table 2). Both members of a pair fed their young throughout the nestling period, but the contribution of the female tended to be greater in the beginning and at the end (Morton, Orejuela and Budd 1972).

The sexes did not appear to differ in their tendency to ingest sacs; rate of consumption was related directly to number of feeding visits. For example, of 864 feedings observed where the sex of the adult was known, 466, or 53.9%, were made by the female. Of 350 observed instances of sac ingestion, 197, or 56.3%, were consumed by the female. According to a chi-square test, these ratios of feeding and sac consumption do not differ ($P > 0.05$).

SAC COMPOSITION

Water content of fecal sacs was highest on Day 0, 83.4%, then decreased slightly thereafter until stabilizing at about 75% on Day 5 (Table 3). From these data and those on rate of sac ingestion, the daily water intake from sacs by parent birds can be computed (Table 3).

The energy content of sacs, as determined by bomb calorimetry, was highest per unit dry weight on Day 0 and decreased to fairly equable values soon thereafter (Table 4). An opposite trend, which I cannot explain, has been found in the Starling (*Sturnus vulgaris*; Westerterp 1973).

The caloric values do not indicate, of course, the metabolizable energy (ME) of sacs, the energy retrievable by the digestive systems of adults. To obtain an estimate of ME, carbohydrate, fat, and protein content of sacs from nestlings of all ages was determined (Fig. 1).

Carbohydrate content of dry sac material was about 2 to 3% in all nestlings. Fat content varied with nestling age, being 7.5% in the Day 0 sample then decreasing to 1 to 2% from Day 3 onward. Protein content was also greatest in the youngest nestlings. The highest value, obtained from the Day 1 sample, was 9.9%, and the lowest was 4.2%, obtained on Day 7. Ash was only 3.7% on Day 0 and varied between 6 and 8% thereafter.

The data in Figure 1 indicate that fecal sacs changed considerably in composition during the first few days of nestling life. Statistical comparisons (t-tests) of data obtained from Day 0 to Day 2 chicks versus Day 3 to Day 9 chicks show that fat, protein, and energy content were significantly higher in the younger group (Table 5).

DISCUSSION

SAC INGESTION AND WATER BUDGET

Net water gain from devoured sacs would occur only if adults were capable of producing more concentrated urine than chicks. Kidney function has not been examined in *Z. l. oriantha* but solute-loaded *Z. l. gambelii* commonly produce urine of 800 mosm (Liu 1972).

TABLE 4. Energy content of fecal sacs of nestling *Z. l. oriantha* (kJ/g dry sac material).

	Nestling age (days)									
	0	1	2	3	4	5	6	7	8	9
Mean	17.84	17.04	17.08	15.83	16.58	16.33	16.41	15.99	16.25	15.12
SD	–	–	0.54	0.08	0.34	0.25	0.80	0.25	0.17	0.59
N	1	2	3	3	3	3	3	3	3	3

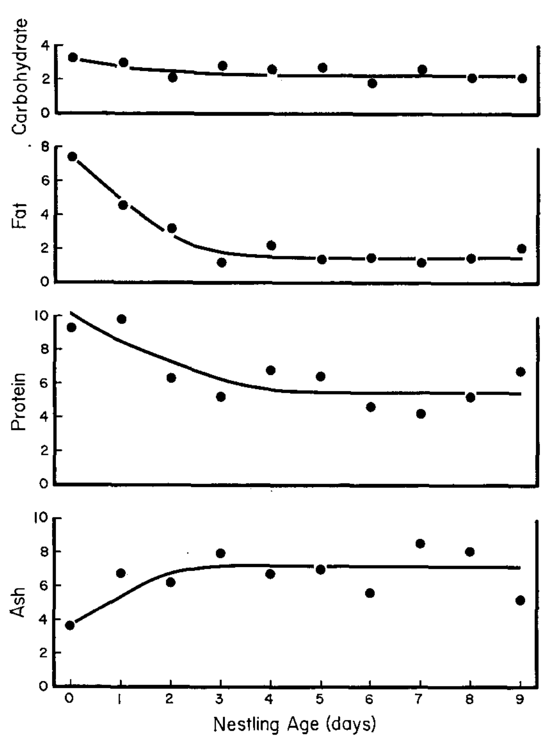

FIGURE 1. Percent of carbohydrate, fat, protein, and ash found in dry fecal material of *Z. l. oriantha* nestlings.

In fact, adult *gambelii* can produce urine as concentrated as 900 mosm and maintain body weight when forced to drink a 0.3 M NaCl solution (Liu 1972). The osmolarity of urine in *Z. l. oriantha* sacs was not measured, but in Roadrunner (*Geococcyx californianus*) nestlings 14 days of age and older it is about 320 mosm (Calder 1968).

Using the data above to represent urine concentrating capacity in these nestling and adult sparrows, we can hypothesize that each gram of urine ingested from sacs represents about 0.6 g of reusable water by adults. Assuming that water content of sacs approximates urine content, we can see from Table 3 that from Day 3 onward, sacs may contribute a net of 3 to 6 g of water per day to each adult. Daily water requirements of a *Z. l. oriantha*-sized bird, not experiencing unusual thermal stress, should be about 7 g per day (Bartholomew and Cade 1963). Thus fecal sacs at times may supply half or more of the daily water needs of adults. In Sierran breeding grounds this would seem to be of little functional significance. Standing and running water were plentiful at all breeding sites I have ever visited and at those described by DeWolfe and DeWolfe (1962). Perhaps water derived from sacs provides an important portion of daily water intake in White-crowned Sparrows nesting in xeric areas such as high plateaus.

SAC INGESTION AND ENERGY BUDGET

Digestive capacities of these nestlings, particularly of fat and protein, appeared to improve markedly during their first four days. This improvement probably represents a post-hatching continuation of gut maturation. Elimination of residual material accumulated in the gut during development in the egg may also contribute to the high fat and protein content of younger nestlings' sacs. The diet of nestlings, primarily insects (Morton, Orejuela and Budd 1972), is undoubtedly rich in these substances also, and it is not surprising that they would be prominent in their feces.

The nutritional value of sacs to adult birds, as opposed to their energy value, is difficult to evaluate. Birds in general need at least 7 to 8% dietary protein for daily maintenance (Martin 1968, Fisher 1972). White-crowned Sparrows may need considerably greater quantities than this to maintain body weight (MacMillen and Snelling 1966), and they probably have drastic energy deficits while feeding nestlings. Their body weights decrease steadily during this time and they may catabolize nearly all of their body fat and even some constituents of the lean body (Morton et al. 1973, Morton 1976).

Knowing the amount of sac material con-

TABLE 5. Statistical comparisons of dry fecal sac components of nestling *Z. l. oriantha*, Days 0–2 versus Days 3–9.

	Age (Days 0–2)			Age (Days 3–9)			
	Mean	SD	N	Mean	SD	N	*P*
Carbohydrate (%)	2.81	0.60	3	2.37	0.38	7	NS
Fat (%)	5.08	2.15	3	1.59	0.44	7	< 0.05
Protein (%)	8.51	1.93	3	5.60	1.02	7	< 0.05
Ash (%)	6.10	1.11	6	7.01	1.52	21	NS
kJ	17.21	0.46	6	15.95	0.63	21	< 0.01

TABLE 6. Metabolizable energy available to adult *Z. l. oriantha* through ingestion of fecal sacs.

	Nestling age (days)									
	0	1	2	3	4	5	6	7	8	9
Female (kJ/day)	1.2	2.1	2.7	4.1	5.9	5.7	6.9	7.3	5.8	4.8
Male (kJ/day)	0.3	1.0	1.7	3.9	4.9	7.0	5.7	5.7	5.1	2.5

sumed per day by parent birds and the proportion of this material that was carbohydrate, fat, and protein, we can calculate metabolizable energy available in sacs to the adults. Assuming the ME derived from carbohydrate or protein ingested by birds is 17.58 kJ/g and that it is 39.78 kJ/g for fat (King and Farner 1961), we see that during the last week that adults are feeding nestlings, they obtain about 4 to 6 kJ/day from sacs (Table 6). Females usually obtain more energy than males from this source because they tend to take sacs slightly more often than males.

How important are sacs as an energy source to parent birds? Mahoney (1976) recently provided detailed information on the daily energy expenditure (DEE) of *Zonotrichia* on their breeding grounds; her model is especially valuable because it provides estimates of DEE over a range of ambient temperatures (T_as). Mean daily T_a (T_{max} + $T_{min}/2$) at Tioga Pass during the breeding season of *Z. l. oriantha* for the four consecutive years of 1969–1972 was 12.8°C. At that T_a, the sparrow's DEE is about 98 kJ/day if one assumes that energy expenditure for somatomotor activity is twice that of basal metabolic rate (Mahoney 1976).

The above information makes it possible to

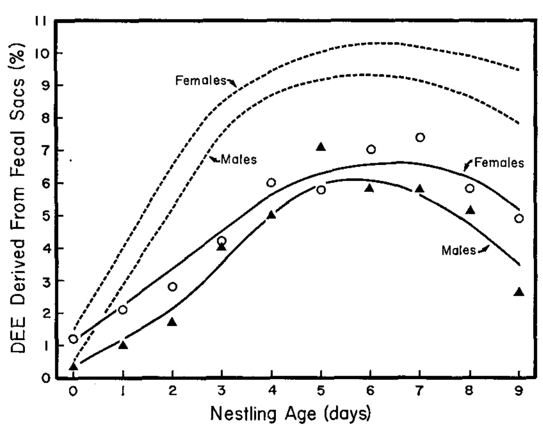

FIGURE 2. Percent of daily energy expenditure (DEE) of adult *Z. l. oriantha* derived from ingesting fecal sacs of their young. Solid curves fitted by eye to data points (circles, females; triangles, males). Dashed curves represent hypothetical DEEs (see text).

evaluate the importance of sac ingestion as an energy source in these birds (Fig. 2). The lower curves (solid lines) were derived from mean sac weights, the upper curves (dashed lines) represent energy available if it is assumed that normal size of sacs is more accurately represented by the heaviest one-third of those collected for assays. Recalling the large range in sac sizes and the collection methods used, this assumption seems reasonable. It follows then that nearly 10% of the adults' DEE, during the last week they have nestlings, may be derived from fecal sacs.

Habitual consumption of sacs, rather than their removal to another place, would seem to engender a certain amount of risk for parent birds. For example, the sacs might contain concentrations of toxic material or infectious stages of parasites. Sacs are consumed, however, and, in *Z. l. oriantha*, without fail. This surely means that, on balance, the behavior is advantageous.

Recycling nutrients in this way may be an important time- and energy-sparing habit that allows adults to give more of the total food gathered to nestlings thereby enhancing the latters' growth and development, possibly important in breeding areas with short summers. Evidence suggests that rate of development in *Z. leucophrys* nestlings increases with latitude and altitude (Morton 1976). A study of fecal sac ingestion habits along latitudinal and altitudinal clines might reveal an example of how a shift in behavior can increase fitness to changing environmental conditions.

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