MINERAL AND NITROGEN CONCENTRATIONS IN FECES OF SOME NEOTROPICAL BATS

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Concentrations of nitrogen and minerals in individual fecal pellets of *Noctilio leporinus* directly reflect composition of the fish, crustaceans, beetles, or moths originally consumed. Among Neotropical bats that feed primarily on plant parts (fruits, nectar, pollen, and flowers), animal parts (insects and vertebrates), or both, differences in measured concentrations of nutrients are present in feces. Nitrogen levels are markedly higher and sodium levels are marginally higher in feces of carnivores and omnivores than in frugivores. Calcium levels are higher and potassium levels are lower in feces of bats that primarily consume insects. Total iron levels in feces of frugivorous species are marginally lower than in carnivores or omnivores. Magnesium concentrations seem unrelated to feeding habits. Intake of nitrogen, potassium, and magnesium appears to be adequate for bats of all feeding habits. Periodic deficiencies for calcium exist for insectivorous species and for sodium, and possibly iron, in some frugivorous species.

Key words: bat, chiroptera, feces, guano, nutrition, feeding habits, mineral, nitrogen

Most nutritional studies of bats have dealt with caloric (energy) needs or water needs (Bassett and Studier, 1988; Kunz and Nagy, 1988). In recent studies of guano of free-living big brown bats, *Eptesicus fuscus,* we examined nitrogen and mineral budgets. Results of those studies suggested there may be mineral deficiencies in this insectivorous species, deficiencies that differ with season, reproductive condition, and gender (Studier et al., 1991) and with location of maternity roost sites (Studier et al., 1994). Most New World temperate-zone bats are insectivorous, in contrast to Neotropical bats, which have highly diverse feeding habits (Wilson, 1988). We expect that, because of their diverse feeding habits, Neotropical bats have nutritional deficiencies that are unlike the deficiencies of insectivorous temperate-zone bats such as *E. fuscus*. This would occur because nitrogen and mineral concentrations will differ extensively between insects and the food of Neotropical bats, so intake of nitrogen and minerals will also differ for temperate zone and Neotropical bats.

The fishing bat or greater bulldog bat, *Noctilio leporinus,* preys on a wide variety of animals, including fish, crustaceans, and insects (Hood and Jones, 1984). We chose *N. leporinus* for the present study because, with its diverse feeding habits, it probably does not have nutritional stress. We also analyzed feces from bat species with other diverse feeding habits. The purpose of this study is to survey the nutritional status of Neotropical bats of varying feeding habits through analysis of feces for nitrogen and mineral (sodium, potassium, calcium, magnesium, and iron) concentrations.

MATERIALS AND METHODS

We collected and analyzed feces from bats at two localities. Guano of *N. leporinus* was collected periodically from 22 May through 26 June 1991 from a screen placed under a colony of at least six male and 20 female bats that roosted in a rock fissure on the island of Culebra, Puerto Rico. About two-thirds of the females in this roost gave birth in mid-June; thus, the pooled sample contained guano from males as well as pregnant and lactating females. Known prey of *N. leporinus* collected during the same time interval include male fiddler crabs (*Uca* sp.) and two species of fish, silversides (*Antherinomorus stipes*) and sardines (Harengula sp.). We used compositional analysis of moths and beetles from southcentral Michigan, because specific moths and beetles eaten by *N. leporinus* on Culebra are unknown, and nutrient composition of beetles and moths from Michigan is likely to be similar to that of such insects from Culebra. All specimens were partially dried in the field or frozen until returned to the laboratory at the University of Michigan-Flint where samples were dried to constant mass at 50–60°C. After preliminary examination of dissected, dried scats, feces were segregated into pellets of moth, beetle, fish, or fiddler crab origin based on color, size, surface presence of fish scales or moth scales, or other exoskeletal components.

Bats were captured in mist nets on consecutive nights from 5 through 23 July 1992 between 1800 and 1930 h local time at several locations near the Explorama Camp, Explorama Lodge or ACEER (Amazon Center for Environmental Education and Research) close to the Amazon and Napo rivers downstream from Iquitos, Peru. Bats were held for 1–3 h in individual 20- by 30-cm burlap or monkscloth bags, identified, examined to determine gender, retained for use in other studies, or released after the bag had been examined for presence of feces. All feces removed from each bag were placed in small, labelled, plastic test tubes and then sealed in ziplock bags partially filled with silica gel desiccant. Each tube containing partially dried, fecal samples was capped, returned to the laboratory, and dried to constant mass at 50–60°C.

Collected dried foods were individually and uniformly ground in a coffee bean grinder. Dried fecal pellets from the Peruvian bat samples, which were or could be freed of adherent cloth fibers, and fecal pellets from *N. leporinus* that had been separated according to content were each gently ground between individual glassine weighing papers with an agate pestle in an agate mortar. We analyzed fecal samples and samples of foods eaten by *N. leporinus* by taking portions (50–100 mg weighed to the nearest 0.1 mg) of each sample. Each portion was digested in a 100-ml volumetric flask with persulfuric acid and 30% H_2O_2 and then diluted to 100 ml. Portions were then analyzed for nitrogen by Nesslerization (Treybig and Haney, 1983) and mineral (sodium, potassium, calcium, magnesium, and iron) content by atomic absorption or flame emission spectrophotometry. For procedural details, see Studier and Sevick (1992). Data were stored in Lotus files and analyzed using SYSTAT (Wilkinson, 1989). When multiple comparisons were made, a Bonferroni correction was used.

No data are presently published on minimal requirements among bats for the various nutrients measured. Because the only data available on minimal requirements for growth and reproduction in small mammals are for rodents studied under laboratory conditions (National Research Council, 1978), those data are used throughout the paper to represent requirements of small mammals, and we assume requirements for bats are comparable.

Results and Discussion

There are three possible interpretations from assessing levels of nutrients in food and feces. If the concentration of a nutrient in feces is greater than in food, that nutrient is assimilated less rapidly than average dry mass and probably exists in excess in that food. If a nutrient concentration in feces is less than in food, that nutrient is being assimilated more rapidly than average dry mass and may be present in minimal or inadequate concentration in that food. A nutrient present in equal concentrations in both food and feces is assimilated at the same rate as average dry mass and that food represents an adequate dietary source.

Iron is poorly assimilated and is routinely present in higher concentrations in feces than in the diet (Charlton and Bothwell, 1983). Some nutrients present in adequate or excessive dietary concentrations, such as sodium, potassium, and nitrogen, are often rapidly assimilated with any excess voided in urine. Since no urine samples were collected for this study, we cannot draw direct nutritional conclusions on that basis.

We assume that nutrients present in high or variable concentrations in feces are also

"DIGESTED fish"= partie des feces identifiee comme fish etc..=

TABLE 1.—*Nitrogen and mineral composition of some typical foods eaten by* Noctilio leporinus *and of feces produced by* N. leporinus *after digesting those foods. Values shown are means* ± SE *in parts per thousand dry mass. Samples are from* Antherinomorus stipes *(silversides),* Harengula *sp. (sardines), male* Uca *sp. (fiddler crabs), and 181 species of lepidopterans (moths) and 43 species of coleopterans (beetles) from southern lower Michigan (Studier and Sevick, 1992). "Required" values are the minimal level of each nutrient required for growth and reproduction among five species of rodents (National Research Council, 1978).*

Source or level	n	Concentrations of elements (parts per thousand dry mass)					
		Ca	Mg	K	Na	Fe	N
Silversides	28	70.76 ± 3.26	4.46 ± 0.15	8.27 ± 0.32	3.60 ± 0.10	0.29 ± 0.02	138.7 ± 1.3
Sardines	43	58.56 ± 2.01	3.16 ± 0.10	9.47 ± 0.17	3.03 ± 0.02	0.76 ± 0.07	149.6 ± 1.6
Digested fish	10	79.05 ± 3.77	8.41 ± 0.81	2.03 ± 0.30	2.54 ± 0.13	1.32 ± 0.50	103.6 ± 4.4
Fiddler crab	28	172.25 ± 2.12	17.02 ± 0.75	3.02 ± 0.13	6.40 ± 0.26	1.71 ± 0.10	72.0 ± 1.6
Digested crab	10	111.97 ± 4.01	19.06 ± 0.77	2.40 ± 0.55	2.95 ± 0.43	2.60 ± 0.17	38.5 ± 7.2
Moth		1.22 ± 0.04	2.31 ± 0.07	9.40 ± 0.13	0.54 ± 0.06	0.15 ± 0.01	166.1 ± 1.3
Digested moth	10	4.77 ± 1.32	10.16 ± 0.31	9.49 ± 0.91	4.87 ± 0.58	0.57 ± 0.27	163.8 ± 4.5
Beetle		1.05 ± 0.05	1.53 ± 0.04	9.01 ± 0.22	1.66 ± 0.10	0.19 ± 0.02	168.4 ± 2.1
Digested beetle	10	4.97 ± 0.21	4.79 ± 0.80	3.83 ± 0.69	2.94 ± 0.28	1.35 ± 0.44	143.1 ± 10.1
"Required"		8.0	1.0	7.2	1.5	0.14	29.0

moth and beetle data from studier and sevick 1992 cf refs to find (data not entered in the template)

present in adequate or excess amounts in dietary items. We also assume that when a nutrient is present in low and non-variable concentrations in feces, all available mechanisms to maximize assimilation of that nutrient are being employed and such nutrients probably are present in minimal or inadequate concentrations in the diet. Such an implication is strengthened if fecal concentrations are lower than estimated minimal requirements for that nutrient.

Elemental nutrition in Noctilio leporinus.—Although foods listed in Table 1 represent only a portion of the diet of *N. leporinus,* ingestion of such a wide variety of foods by these bats likely yields highly variable concentrations of the elements studied. This possibility is supported by our results, as feces formed by bats eating fish, crustaceans, beetles, and moths (Table 1) differed significantly in concentrations of each element studied (for iron, $F = 4.664$; calcium, $F = 288.2$; magnesium, $F = 66.76$; potassium, $F = 25.35$; sodium, $F = 6.390$; and, nitrogen, $F = 56.92$; in each case, $d.f. = 3,36$ and $P < 0.008$). At least one potential food for *N. leporinus,* as expected, exceeds their probable need for each nutrient (Table 1).

The fish analyzed seem to exceed probable requirements for each measured nutrient. Fecal concentrations of magnesium, calcium, and iron, all of which exceed respective levels in fish, support the probability that fish represent adequate sources of those minerals. Nitrogen, as urea from protein catabolism, and sodium are prevalent in bat urine (Studier and Wilson, 1983; Studier et al., 1983), so we cannot conclude from the slightly lower concentrations of those elements in feces, compared with concentrations in fish, that fish are inadequate dietary sources of those nutrients, especially since measured levels in both fish and feces exceed likely needs. Potassium is also a prevalent urinary cation (Studier and Wilson, 1983; Studier et al., 1983). The low concentration of that mineral in feces, coupled with the observation that potassium levels in fish approximate the probable potassium requirement of these bats, suggests that fish may represent minimal dietary sources of potassium for *N. leporinus.*

Although fish and insects are routinely consumed throughout the year by *N. leporinus* at the study site, male fiddler crabs and other crustaceans are consumed irregularly in small quantities (Brooke, 1994).

Fiddler crabs are inadequate sources of dietary potassium, may be adequate nitrogen sources, but contain massive amounts of the other mineral nutrients measured. Consumption of small amounts of fiddler crab would readily supplement requirements for those nutrients if other dietary items were inadequate.

As Studier et al. (1991, 1994) described for *E. fuscus,* insects are inadequate sources of calcium, excellent sources of nitrogen and magnesium, and marginal sources of potassium, iron, and sodium (Table 1). Because iron routinely is poorly assimilated, occurrence of higher concentrations of iron in feces than in food is expected (Keeler and Studier, 1992). Higher levels of potassium in feces resulting from consumption of lepidopterans suggest that they are an adequate source of the mineral, but coleopterans may not be. Alternatively, coleopterans contain higher levels of sodium than do lepidopterans.

By routinely consuming insects and fish with occasional supplements of crustaceans, *N. leporinus* would be well-nourished with respect to the nutrients measured, with the possible exception of potassium.

Elemental nutrition in other bats.—We found no differences between sexes in nitrogen or mineral composition of feces in the Peruvian species, so we combined results for males and females (Table 2). These results were unexpected; previously, we found differences between sexes, especially in calcium levels of insectivorous species (Studier et al., 1991). The lack of differences can be attributed either to lack of, or to mixed, reproductive activity among females during the sampling period or to consumption of small amounts of other food items by those bats.

We conclude, based on possible requirements (Table 1) and fecal samples (Table 2), that bats that include foods of animal origin in their diet certainly ingest adequate levels of dietary nitrogen, and even species that feed primarily on plant parts, with the possible exception of *Platyrrhinus infuscus,* seem to maintain positive nitrogen budgets. Levels of fecal nitrogen directly reflect dietary concentrations of nitrogen or the fraction of the diet of animal origin. Those portion of plants consumed by bats are routinely low in nitrogen (Consumer Nutrition Center, 1982). As sole food sources, most plant parts probably would provide inadequate dietary nitrogen; however, some bats have adapted to such low intake of nitrogen (Howell, 1974). Also, supplementing a staple diet of fruit, nectar, or flowers with small amounts of insects (Gardner, 1977) would provide adequate, overall dietary nitrogen.

Of the minerals analyzed, all bats seem to ingest more than adequate dietary concentrations of magnesium, regardless of feeding habits (Table 2). Poor assimilation rates for iron (Charlton and Bothwell, 1983) should be accompanied by levels of fecal iron exceeding dietary requirements and intake as seen in Table 2, which suggests that some frugivorous species may ingest marginally adequate levels of iron. Differences in concentration of total iron in feces of the *Carollia* studied (Table 2) suggest differences in specific foods eaten by these sympatric congeners. As is typical of plants, those parts eaten by bats contain high concentrations of potassium and low concentrations of sodium (Consumer Nutrition Center, 1982); however, levels of those minerals, especially sodium, are highly variable in insects (Studier and Sevick, 1992). High concentration of potassium in the diet is reflected by high concentrations of that mineral in feces of the frugivores tested. Somewhat lower levels of fecal potassium in insectivorous species and in *Trachops cirrhosus* still exceed probable dietary needs (Table 2). Low concentrations of fecal sodium found for many frugivorous species suggest that many frugivores experience at least periodic dietary sodium deficiency. Insectivorous and omnivorous species examined may also ingest marginally adequate levels of sodium (Table 1). Calcium showed the greatest variability in fecal

TABLE 2.—*Nitrogen and mineral concentrations (in parts per thousand dry mass) in feces of some Neotropical bats. Values shown are means* ± SE. *Food habits: I = insectivorous, O = omnivorous, H = herbivorous. Sample sizes are shown for each sex (M = male, F = female). Food habits are derived mostly from Gardner (1977).* n entered in template = sum n_F, n_M

Species	Food habit	*n*		Concentrations of elements in feces (parts per thousand dry mass)					
		M	F	Ca	Mg	K	Na	Fe	N
Saccopteryx bilineata	I	4	5	4.59 ± 0.97	5.09 ± 0.41	16.97 ± 2.32	1.15 ± 0.29	1.63 ± 0.19	133.1 ± 2.2
Mimon crenulatum	I	5	6	1.42 ± 0.21	10.24 ± 0.96	33.24 ± 7.32	1.44 ± 0.31	1.82 ± 0.18	139 ± 3.5
Phyllostomus elongatus	O	8	8	7.25 ± 2.19	8.65 ± 0.70	34.24 ± 4.22	1.04 ± 0.24	1.30 ± 0.10	123.9 ± 5.6
Phyllostomus hastatus	O	8	10	24.95 ± 4.98	9.10 ± 0.64	26.60 ± 2.90	1.38 ± 0.24	1.72 ± 0.32	86.7 ± 8.9
Tonatia bidens	O		2	9.84 ± 5.54	8.94 ± 2.28	46.95 ± 11.63	3.19 ± 0.49	1.63 ± 0.25	105.6 ± 24.7
Trachops cirrhosus	O		2	70.07 ± 40.90	16.55 ± 1.02	17.25 ± 1.85	2.10 ± 0.93	1.30 ± 0.49	109.7 ± 5.7
Glossophaga soricina	H	4	5	28.84 ± 6.94	10.23 ± 1.69	40.48 ± 7.33	0.82 ± 0.23	1.80 ± 0.43	77.4 ± 6.5
Carollia castanea	H	11	12	61.71 ± 6.06	9.67 ± 0.41	27.28 ± 2.40	1.22 ± 0.20	0.51 ± 0.05	52.9 ± 1.3
Carollia brevicauda	H	12	12	35.08 ± 6.94	8.37 ± 0.51	31.16 ± 3.24	0.80 ± 0.18	0.39 ± 0.03	62.7 ± 3.4
Carollia perspicillata	H	14	13	27.86 ± 3.36	7.60 ± 0.65	66.48 ± 8.83	0.60 ± 0.09	1.36 ± 0.32	69.6 ± 3.5
Rhinophylla pumilia	H	4	7	24.57 ± 5.81	9.52 ± 1.08	36.40 ± 3.60	0.96 ± 0.17	0.92 ± 0.09	57.9 ± 4.2
Artibeus glaucus	H	2	3	35.97 ± 14.70	12.38 ± 1.09	30.75 ± 5.09	0.77 ± 0.17	0.71 ± 0.13	60.9 ± 7.3
Artibeus jamaicensis	H	8	6	31.47 ± 6.24	9.07 ± 0.88	35.76 ± 5.50	0.67 ± 0.09	0.74 ± 0.07	55.7 ± 5.4
Artibeus lituratus	H	2	1	24.75 ± 7.89	8.02 ± 0.50	46.89 ± 13.73	0.39 ± 0.24	0.49 ± 0.06	66.4 ± 11.2
Arbiteus obscurus	H	1	1	16.07 ± 7.16	7.72 ± 0.04	40.47 ± 15.01	0.45 ± 0.10	0.62 ± 0.18	49.8 ± 10.7
Platyrrhinus helleri	H		2	50.29 ± 3.28	13.95 ± 0.06	33.57 ± 1.27	1.12 ± 0.58	1.29 ± 0.04	45.1 ± 1.7
Platyrrhinus infuscus	H		2	17.52 ± 1.35	10.99 ± 0.88	65.30 ± 0.64	0.37 ± 0.01	0.56 ± 0.06	26.4 ± 2.1
Uroderma bilobatum	H		2	21.97 ± 4.35	13.08 ± 3.86	66.23 ± 4.75	1.32 ± 0.73	0.98 ± 0.24	53.6 ± 9.4
Sturnira lilium	H	1	3	38.25 ± 18.56	11.80 ± 0.73	63.73 ± 23.54	1.47 ± 0.26	1.05 ± 0.25	60.4 ± 7.8
Myotis riparius	I	2	3	4.91 ± 1.74	9.51 ± 0.36	27.33 ± 4.16	1.73 ± 0.39	1.94 ± 0.19	137.4 ± 3.7

concentrations among the species analyzed. Concentrations of fecal calcium from insectivorous species (<5 ppt dry mass; Table 2) suggest that these Neotropical species suffer periodic inadequate dietary intake of calcium, as do temperate zone insectivorous species (Studier et al., 1991, 1994). Ingestion of vertebrate prey (Gardner, 1977) explains the high level of fecal calcium found for *T. cirrhosus,* and the concentration compares well with values for feces from *N. leporinus,* when consuming vertebrate prey (Tables 1 and 2). Concentrations of calcium found in feces from frugivores imply that their foods contain more than adequate amounts of dietary calcium (Table 2).

Low levels of calcium, coupled with high levels of nitrogen, found in the few fecal samples of the omnivore, *Tonatia bidens,* suggest that the individuals tested had consumed large quantities of insects just previous to capture. Among the omnivorous *Phyllostomus* sp. tested, higher levels of calcium and lower levels of nitrogen in fecal samples from *P. hastatus* suggest that plant parts composed a greater proportion of the diet of *P. hastatus* than for *P. elongatus* at the time of testing.

Our data demonstrate that, in both omnivorous species and bats with more obligate or restrictive feeding habits, fecal composition directly reflects foods recently consumed. Bats with restrictive feeding habits are more likely to exhibit periodic nutrient deficiencies than species with more diverse food habits. Although fecal levels of nitrogen are variable, bats of all feeding habits appear to ingest adequate nitrogen, but species that feed primarily on plant parts probably supplement dietary nitrogen by consuming some insects. The most probable periodic deficiencies in the mineral nutrients measured here are for calcium in insectivorous species and for sodium in phytophagous or frugivorous species.

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