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Keystone resource (*Ficus*) chemistry explains lick visitation by frugivorous bats

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Geophagy is a widespread behavior among plant-eating animals. In the Neotropics, mineral licks are activity hot spots for frugivorous bats (Stenodermatinae). Bats drink mineral-rich water accumulated in soil depressions made by geophagous mammals. Two mechanistic hypotheses have been proposed to explain this behavior: licks are reliable sources of limiting nutrients, especially sodium; and licks provide substances that render dietary toxins less harmful. We assessed the former by examining bats' diets in conjunction with lick chemistry in the Peruvian Amazon. We found that most bats that visit licks belong to the subfamily Stenodermatinae and are specialists on *Ficus* fruits—a keystone resource. In addition, although *Ficus* fruits are good sources of some minerals, their sodium content is limited in relation to the physiological requirement of a small mammal. In contrast, bats of the subfamily Carolliinae supplement their fruit diets with insects, potential sources of sodium. Complementary results among diets, *Ficus* chemistry, and lick-water chemistry strongly support the sodium-limitation hypothesis for bat lick use and suggest a mechanistic link between bats and ecosystem engineers that make soil-borne resources available. Because sodium is an essential nutrient for vertebrates and *Ficus* is a keystone resource for many animal species, our results may have implications for the community of frugivorous vertebrates in areas where sodium is limited. Licks may play a critical role as sodium sources and thus they should be considered as important conservation targets.

Key words: Amazonia, bats, Carolliinae, figs, limiting resources, mineral licks, sodium, Stenodermatinae

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Geophagy, the deliberate consumption of soil, is a widespread behavior among plant-eating animals (Gilardi et al. 1999; Klaus and Schmid 1998; Krishnamani and Mahaney 2000; Lee et al. 2010). This unique phenomenon has captured the attention of researchers, who have attempted to determine its underlying mechanisms. As a result, a set of hypotheses ranging from physiological to social explanations has been proposed (Burger and Gochfeld 2003; Davies and Baillie 1988; Gilardi et al. 1999; Klaus and Schmid 1998; Mahaney et al. 1995).

In the Neotropics, natural soil licks are activity hot spots for several frugivorous bats that drink water that accumulates in puddles (Bravo et al. 2008, 2010b) created by geophagous mammals (Izawa 1993; Klaus and Schmid 1998; Tobler et al. 2009). Even though eating soil and drinking water differ in whether the bulk of the ingested material is solid versus liquid, 2 non–mutually exclusive, mechanistic hypotheses have been proposed to explain these behaviors: licks are reliable sources of limiting nutrients, especially sodium (Bravo et al. 2010b; Brightsmith et al. 2008; Emmons and Stark 1979; Powell et al. 2009); and licks provide substances that render dietary toxins less harmful (Brightsmith et al. 2008; Gilardi et al. 1999; Voigt et al. 2008). These hypotheses have mainly been addressed by examining characteristics of soil or water preferred by animals that visit licks (Bravo et al. 2010a, 2010b; Brightsmith and Aramburú 2004; Emmons and Stark 1979; Izawa 1993; Powell et al. 2009; Wilson 2003). However, few studies have examined the organisms' diets in conjunction with substances consumed at licks (e.g., Brightsmith et al. 2008; Gilardi 1996). Here, we studied a group of Neotropical frugivorous phyllostomatid bats (Stenodermatinae) whose members in the southeastern Peruvian Amazon regularly visit natural soil licks to drink water that has accumulated in puddles (Bravo et al. 2008, 2010b) and compared them to related species (Carolliinae) that rarely visit licks, to determine whether the chemistry of preferred fruits is consistent with the nutrient-limitation hypothesis.

Although frugivorous bats of the subfamilies Carolliinae and Stenodermatinae (family Phyllostomidae) are common in Neotropical assemblages (Gardner 2008), puddles at licks are visited nearly exclusively by stenodermatine bats (Bravo et al. 2010b; Voigt et al. 2007). Reproductive females visit licks out of proportion to their relative abundances in their respective populations (Bravo et al. 2008, 2010b; Voigt et al. 2007).

The striking difference in visitation patterns to licks by carolliine and stenodermatine bats coincides with a striking difference between their general diets, at least as reported in the literature. Most stenodermatines are consistently reported to specialize on *Ficus* fruits (Ascorra et al. 1996; Giannini and Kalko 2004; Kalko et al. 1996)—keystone resources in Neotropical forests (sensu Terborgh 1986). *Sturnira* species are exceptions to this general pattern, because they feed mainly on *Solanum* fruits (Fleming 1986). In contrast, carolliines are consistently reported to be *Piper* specialists (Ascorra et al. 1996; Fleming 1988; Giannini and Kalko 2004). Both the nutrient-limitation and the dietary-toxin hypotheses could be consistent with these dietary patterns. If nutritional requirements are not met by—or dietary toxins are present in—the diets of lick-visiting stenodermatines, members of that group may seek substances (e.g., mineral nutrients or clay) at licks, especially during reproduction, that is, periods of high nutritional demand (Barclay and Harder 2003; Nelson et al. 2005).

Licks are sources of mineral-rich water (Bravo et al. 2010b; Izawa 1993). Lick water contains a consistently high concentration of selected minerals, especially sodium, in comparison to other water sources also available to bats in regions where licks are found (Bravo et al. 2010b). Bravo et al. (2010a) also showed experimentally that stenodermatine bats prefer lick water over other water sources. Thus, it is very likely that lick water provides 1 or more important resources to bats.

Determining the nutritional quality of plant species consumed by carolliine and stenodermatine bats should provide additional insights into which substances bats may be seeking at licks. In particular, low concentrations of key mineral nutrients in the diets of lick-visiting stenodermatines compared to nonvisiting carolliines would support the nutrient-limitation hypothesis. Accordingly, here we address the hypothesis that key minerals are limited in diets of stenodermatine bats in the Peruvian Amazon. We determined the diet compositions of 22 bat species and assessed their correlation with lick visitation. We also determined the nutritional composition of *Ficus* and *Piper* fruits collected in the area of study and analyzed the concentrations of 4 key minerals, as well as nitrogen (as a measure of protein).

MATERIALS AND METHODS

Study site.—We conducted this study at Los Amigos Conservation Concession in Madre de Dios, southeastern Peruvian Amazon (12°30′–12°36′S, 70°02′–70°09′W). This private concession protects >140,000 ha of lowland tropical forest. Average annual temperature for 2005–2007 ranged from 23.9°C to 24.1°C, and annual rainfall ranged from 2,152 to 2,682 mm.

Bats' associations with licks.—To determine whether there was a bias by stenodermatine bat species for visiting licks, we compared bat assemblages at licks, forest, and gap sites using species' abundances at each site, as in Bravo et al. (2010b), but supplemented with an analysis of similarity (Magurran 2004). A visual representation of similarities among bat assemblages sampled at lick and nonlick sites was generated with a nonmetric multidimensional scaling analysis, using Bray–Curtis dissimilarities (Gotelli and Ellison 2004). We also compared the total abundances of each bat species captured among site types (lick, forest, or gap; data from Bravo et al. [2010b]) using a goodness-of-fit *G*-test, for species with expected values larger than 5 individuals (Sokal and Rohlf 1995). To handle and process bats in this study, we followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and protocol 08-017 approved by the Institutional Animal Care and Use Committee from Louisiana State University.

Fecal samples and diet analyses.—To characterize bats' diets, we collected fecal samples from bats captured at 3 places along the Los Amigos River. At each place from September to November 2005, we captured bats at a lick and a forest site. From July to September 2007 and February to April 2008 we added a gap site to each lick–forest pair. At licks, we used a single 6-m mist net, which generally captured bats at a rate that allowed 2 or 3 people to process them. At gap and forest sites we deployed five to ten 6-m mist nets along previously opened trails. We opened the nets from dusk (~1730 h) to midnight (2400 h). Because of the large numbers of bats at licks, we closed and reopened those nets as necessary (see Bravo et al. [2008, 2010b] for more-detailed information about sites and methods used to capture bats). After capture, each bat was aged, identified, measured, sexed, and weighed. In addition, we collected fecal samples from the cotton bag where the bat was kept temporarily (no more than 30 min).

Items identified in fecal samples using a dissecting microscope were classified as insects, pulp, seeds, or soil. With the assistance of an experienced field botanist, seeds were classified as *Cecropia* (Moraceae), *Ficus* (Moraceae), *Philodendron* (Araceae), *Piper* (Piperaceae), *Solanum* (Solanaceae), *Vismia* (Clusiaceae), family Cucurbitaceae, or undetermined species. Because of small sample sizes (8% of total fecal samples collected), we grouped samples with seeds of *Philodendron*, *Solanum*, *Vismia*, and Cucurbitaceae into 1 category for analysis. To determine whether stenodermatine bats were associated with a particular diet, we examined the relationship between diet composition (*Cecropia*, *Ficus*, *Piper*, insects, etc.) and bat species using a correspondence analysis for all fecal samples collected across all sites (Gotelli and Ellison 2004). Then, because of our particular interest in the diets of frugivorous bats of the subfamilies Carolliinae and Stenodermatinae, we grouped bats as carolliines, stenodermatines, and "others." Next, we compared the proportion of each item in the diet across bat subfamilies using generalized linear models with Poisson distributions (Crawley 2007). We tested the effect of diet–subfamily interaction by comparing a saturated model with a model without the interaction using an analysis of deviance that used a chi-square test (Crawley 2007). We then tested the equality of proportions of the most common food items (*Cecropia*, *Ficus*, and *Piper*) for each bat group using a goodness-of-fit *G*-test (Sokal and Rohlf 1995).

Fruit sampling and analyses.—From February to April 2008 and July to August 2008, we collected ripe fruits from *Ficus* and *Piper* species. Twice a week 1 of us (AB) systematically walked along the approximately 50-km trail system of the Los Amigos Biological Station, which covers both floodplain and terra firme forest. We collected intact ripe *Ficus* fruits from beneath the crowns of fig trees. We collected ripe infructescences (maturity of fruits was gauged by their softness) directly from adult individuals of *Piper* species. On a given walk, when no ripe infructescences were found, we enclosed unripe ones with a soft mesh cloth to prevent bat consumption until they became soft and were collected a few days later. We collected botanical samples to identify each plant to species. We oven-dried fruits at ~60°C for ~15 h. Dried fruits were analyzed for 12 elements (boron, calcium, copper, iron, magnesium, manganese, nitrogen, phosphorus, potassium, sodium, sulfur, and zinc) by the Soil Testing and Plant Analysis Laboratory at the Louisiana State University Agricultural Center (http://www.lsuagcenter.com) using the following procedure. First, 5 ml of concentrated HNO_3 was added to a minimum of 0.5 of g ground, dry plant matter. Second, after 50 min, 3 ml of H_2O_2 was added and the sample was digested on a heat block for 2.75 h. Finally, samples were cooled and diluted to measure the concentration of minerals using inductively coupled plasma spectrometry. Although we were interested in the mineral content of fruits, we also determined the concentration of nitrogen because of increased protein demand during reproduction (Speakman 2008; Studier and Wilson 1991). Nitrogen concentration was analyzed via dry combustion of a 0.1-g sample using a Leco carbon–nitrogen analyzer (Leco Corp., St. Joseph, Michigan). Concentrations were provided in parts per hundred (%) for most minerals. Sodium and nitrogen concentrations were provided in parts per million (ppm). For comparative purposes we converted parts per hundred to parts per million when necessary.

We explored patterns of both mineral and nitrogen concentrations among fruits of *Ficus* and *Piper* with a principal component analysis (Gotelli and Ellison 2004). In addition, using an a priori contrasts analysis of variance (Gotelli and Ellison 2004), we compared the concentrations of nitrogen and 4 key minerals (calcium, magnesium, potassium, and sodium) between *Ficus* and *Piper* species. We adjusted the alpha level for all contrasts using the Bonferroni correction method (Gotelli and Ellison 2004). All statistical analyses were performed in R (R Development Core Team 2007).

RESULTS

Bat species' associations with licks.—Stenodermatine bats showed a strong preference for natural soil licks. There was a significant difference between the bat assemblage at licks compared to the ones at forest ($R = 0.94$, $P = 0.001$) and gap ($R = 0.96$, $P = 0.001$) sites. On the other hand, there was no significant difference between the bat assemblages at forest and gap sites ($R = 0.05$, $P = 0.28$; Fig. 1). These specific results are supported by tables presented in Appendices I-VI. Sixteen of 17 stenodermatine species analyzed were overrepresented at licks compared to nonlick site types (Fig. 2; Appendix V). In contrast, *Carollia brevicauda* and *C*. *perspicillata* were more common in forest sites and gaps compared to licks (Fig. 2; Appendix V).

Composition of bats' diets.—We collected a total of 245 bat fecal samples: 103 samples from 16 bat species captured at natural soil licks, 60 from 12 species captured at forest sites, and 82 from 10 species captured at gaps. At licks, samples were obtained from 15 frugivores of the family Phyllostomidae: 2 carolliines and 13 stenodermatines (Appendix IV). At forest sites and gaps, all but 1 fecal sample belonged to bats of the family Phyllostomidae. Fecal samples from *Carollia* species were common in forest and gap site types (63% and 88% of total samples, respectively) and rare at licks (~3% of total samples; see Appendixes IV–VI).

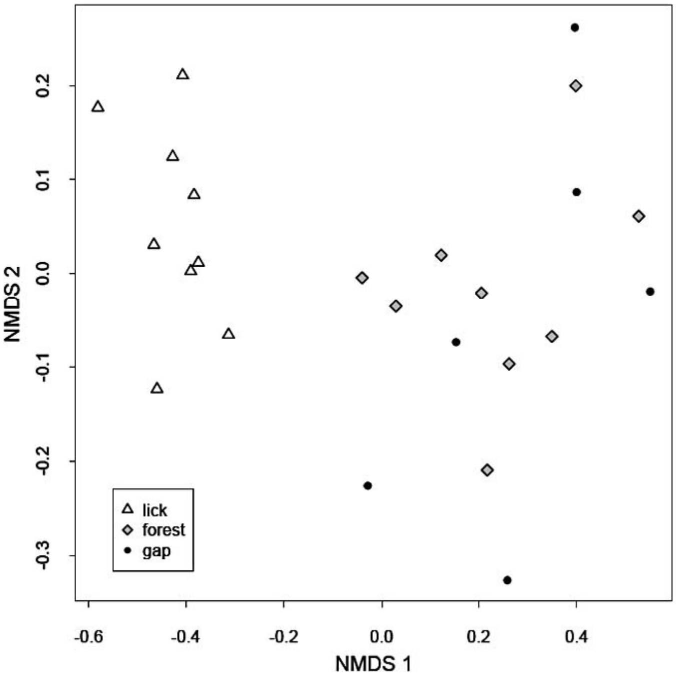

FIG. 1.—Ordination plot for assemblages of bats captured at lick, forest, and gap sites using a nonmetric multidimensional scaling analysis (stress = 9.83).

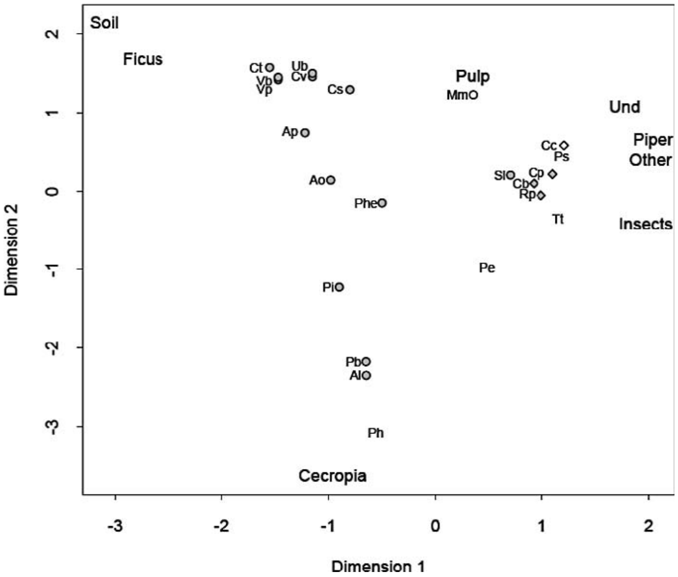

FIG. 2.—Ordination plot for the correspondence analysis of 22 bat species and 8 dietary items. Bat species are abbreviated as *Artibeus lituratus* (Al), *A. obscurus* (Ao), *A. planirostris* (Ap), *Carollia brevicauda* (Cb), *C. castanea* (Cc), *C. perspicillata* (Cp), *Chiroderma salvini* (Cs), *C. trinitatum* (Ct), *C. villosum* (Cv), *Mesophylla macconnelli* (Mm), *Phyllostomus elongatus* (Pe), *P. hastatus* (Ph), *Platyrrhinus brachycephalus* (Pb), *P. helleri* (Phe), *P. infuscus* (Pi), *Phylloderma stenops* (Ps), *Rhinophylla pumilio* (Rp), *Sturnira lilium* (Sl), *Thyroptera tricolor* (Tt), *Uroderma bilobatum* (Ub), *Vampyriscus bidens* (Vb), and *Vampyriscus pusilla* (Vp). The "Other" category of diet includes seeds of Araceae, Clusiaceae, Cucurbitaceae, and Solanaceae, and "Und" accounts for undetermined species. Circles and diamonds indicate stenodermatine and carolline bats, respectively. Gray circles indicate bat species overrepresented at licks ($P < 0.001$), whereas gray diamonds show bat species underrepresented at licks compared to nonlick sites ($P < 0.001$). G-values and number of bats at each site are presented in Appendix II.

There was a clear distinction between the diets of carolliine and stenodermatine species. Most stenodermatine species clustered as *Ficus* specialists, whereas all carolliine species clustered toward a more diverse diet, mostly composed of *Piper* but complemented with insects and other fruits (Fig. 2). Eight fecal samples from 5 stenodermatine species captured at licks also contained small amounts of soil. None of the carolliine fecal samples contained obvious soil. In addition, there was a significant interaction between diet composition and the bats' groupings (carolliine, stenodermatine, and "other;" $D_{14} = 183.14$, $P < 0.01$). Stenodermatine bats preferred *Cecropia* ($G_2 = 23.6$, $P < 0.001$) and *Ficus* ($G_2 = 109.9$, $P < 0.001$), whereas *Carollia* species preferred mostly *Piper* ($G_2 = 84.8$, $P < 0.001$) fruits.

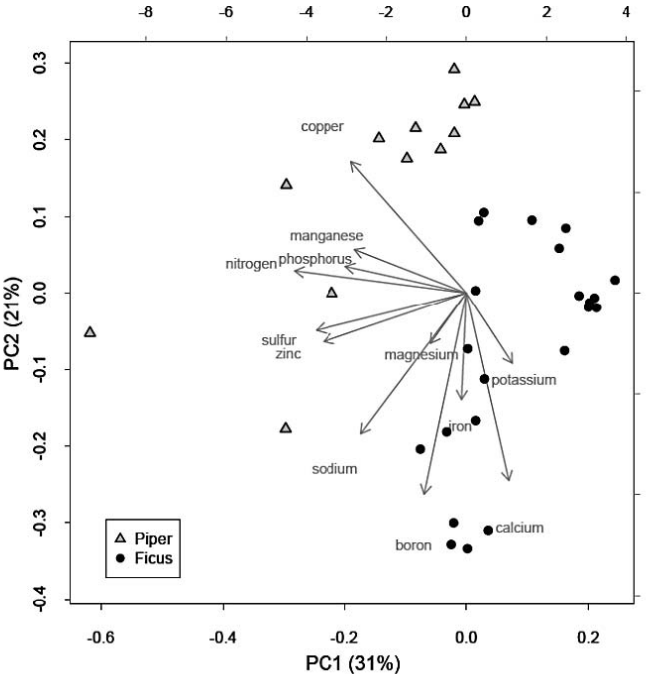

FIG. 3.—Biplot for the two 1st principal components from the principal component analysis of nutrient content of *Ficus* and *Piper* fruits.

Mineral and nitrogen concentration in Ficus versus Piper species.—*Ficus* and *Piper* fruits differed in their mineral and nitrogen contents ($n = 10$ *Ficus* species and 6 *Piper* species; Fig. 3; see Appendix I for concentration values). From the principal component analysis ~50% of the total variation was explained by the first 2 components. Principal component 1 explained 31%, whereas principal component 2 explained 21% (Fig. 3). Nitrogen and sulfur contributed the most to principal component 1 (loadings –0.476 and –0.415, respectively), whereas boron and calcium were most influential for principal component 2 (–0.54 and –0.504, respectively; Appendix III).

Ficus fruits had higher concentrations of calcium and potassium compared to *Piper* fruits (Ca: $t_1 = 22.92$, $P < 0.001$; K: $t_1 = 5.50$, $P < 0.001$). In contrast, *Piper* fruits had higher concentrations of nitrogen compared to *Ficus* fruits ($t_1 = –14.90$, $P < 0.001$). No significant differences were found in the concentrations of magnesium ($t_1 = –1.09$, $P = 0.3$) and sodium ($t_1 = –2.45$, $P = 0.03$; Table 1).

DISCUSSION

Stenodermatine bats as Ficus specialists.—Most stenodermatine bats in southeastern Peru are *Ficus* specialists. In spite of the fecal sample size collected (245 samples) relative to the total number of bats captured (2,409 individuals—Bravo et al. 2010b), the consistency in dietary composition suggests that most stenodermatine species in southeastern Peru are *Ficus* specialists, consistent with other dietary studies in Panama (Giannini and Kalko 2004). Stenodermatines also had a strong preference for licks compared to other common phyllostomid bats (i.e., carolliine bats—Bravo et al. 2008, 2010b).

Contrary to stenodermatine bats, carolliine species had a more diverse diet. *Carollia* spp. were associated with a diet composed mainly by *Piper* species (as suggested by Fleming [1988] and Giannini and Kalko [2004] for Central America), but complemented with other fruit species and insects (as found

Table 1.—Maximum, minimum, and average mineral (calcium [Ca], magnesium [Mg], potassium [K], and sodium [Na]) and nitrogen (N) concentrations in *Ficus* and *Piper* fruits. Results of the contrasts analysis of variance between genera are shown by the *P*-values. An asterisk (*) indicates significant differences for alpha values corrected by the Bonferroni method. % = parts per hundred, ppm = parts per million.

	Ficus					*Piper*					
Units	Maximum	Species	Minimum	Species	Average	Maximum	Species	Minimum	Species	Average	*P*
Ca (%)	1.808	*Ficus insipida*	0.240	*Ficus* sp. 5	0.796	0.599	*Piper* sp. 2	0.115	*Piper augustum*	0.269	<0.01*
Mg (%)	0.403	*Ficus americana*	0.121	*Ficus jurunesis*	0.258	0.430	*Piper* sp. 1	0.203	*Piper* sp. 5	0.256	0.30
K (%)	2.671	*Ficus* sp. 1	1.073	*Ficus americana*	1.876	1.955	*Piper augustum*	1.270	*Piper* sp. 2	1.637	<0.01*
Na (ppm)	39.391	*Ficus maxima*	5.077	*Ficus* sp. 4	17.403	46.000	*Piper* sp. 2	5.182	*Piper* sp. 5	20.628	0.03
N (%)	1.512	*Ficus maxima*	0.791	*Ficus juruensis*	1.202	2.759	*Piper* sp. 3	1.435	*Piper* sp. 5	1.757	<0.01*

by York and Billings [2009]). *Carollia* spp. are usually common in open areas, such as gaps, where *Piper* plants are common (Dumont 2003; Thies and Kalko 2004). However, neither *Carollia* spp. nor *Piper* plants were common at licks (open areas). *Piper* plants were not common, possibly because of the frequent trampling of small plants by larger geophagous mammals (A. Bravo, pers. obs.). The low number of *Carollia* spp. found at licks suggests that they do not need lick water as much as do stenodermatine bats.

Carolliine and stenodermatine bats also feed on *Cecropia*, a relatively abundant tropical genus of trees that produces fruits continuously throughout the year (Dumont 2003). It is also known that frugivorous bats consume some large-seeded plant species (Lobova et al. 2009), seeds of which cannot pass through the bats' guts. Although we recorded the presence of pulp in fecal samples, the contribution of large-seeded fruits may be underestimated. However, many studies have demonstrated that *Ficus* and *Piper* species constitute the main component of stenodermatine and carolliine diets, respectively (Ascorra et al. 1996; Giannini and Kalko 2004; Gorchov et al. 1995), likely because contrary to large-seeded species, *Ficus* and *Piper* fruits are available year-round (Janzen 1979; O'Brien et al. 1998; Terborgh 1986).

Ficus and Piper nutritional patterns.—*Ficus* and *Piper* species clearly differed in their nitrogen and mineral concentrations. Nitrogen, the main constituent of proteins (Morris 1991), was present in higher concentrations in *Piper* fruits than in *Ficus* fruits. Herbst (1986) and Fleming (1988) likewise presented evidence for a similar pattern of nitrogen concentrations in *Piper* compared to other fruit species in Central America. However, although some studies have suggested that bats cannot obtain sufficient proteins from *Ficus* fruits compared to *Piper* (Herbst 1986; Morrison 1980; Studier and Wilson 1991), Wendeln et al. (2000) found higher concentrations of protein in *Ficus insipida* (7.9% in dry pulp and 8.5% in seeds) than previously reported, concluding that *Ficus* was a good source of protein (nitrogen) for bats. In southeastern Peru, concentrations of nitrogen in *Ficus* and *Piper* species are higher than in Central America. Thus, frugivorous bats in that region seem to acquire adequate amounts of nitrogen and protein from their fruit sources.

Ficus fruits are rich in calcium. They have higher calcium concentrations than *Piper* fruits. This calcium-rich pattern for *Ficus* has been reported for species from around the tropics (Gilardi 1996; Nagy and Milton 1979; O'Brien et al. 1998; Wendeln et al. 2000). Therefore, it is unlikely that *Ficus*-specialist bats (stenodermatines) face calcium constraints from having a fruit diet. Although *Piper* fruits contain lower calcium than *Ficus* fruits, they have enough for *Carollia* spp. to meet calcium demands of small mammals (5,000 ppm for mice—National Research Council 1995). Furthermore, stenodermatine as well as carolliine species consume *Cecropia* fruits, which often contain high concentrations of calcium (13,300 ppm—Nagy and Milton 1979). Accordingly, frugivorous bats in southeastern Peru seem able to meet their needs of calcium from their fruit diets.

Unlike calcium, fruits in the southeastern Peruvian Amazon have significantly lower sodium concentrations than fruits in other tropical regions (Appendix III). Similar to Gilardi (1996), who reported 28.86 ppm ± 21.02 *SD* of sodium for 8 *Ficus* species collected in southeastern Peru, we found an average of 17.4 ± 11.5 ppm and 20.63 ± 15.96 ppm for *Ficus* and *Piper* fruits, respectively. In general, it is expected for most plants to contain low concentrations of sodium because contrary to vertebrates, physiologically plants require low concentrations of sodium (Morris 1991). However, compared to other sites in the tropics (Nagy and Milton 1979; O'Brien et al. 1998; Wendeln et al. 2000), sodium seems to be more limited in fruits of southeastern Peru. In Central America, Wendeln et al. (2000) reported a sodium concentration ~100 times higher in *Ficus* fruits (1,690 ppm average for 14 *Ficus* spp.) than what we found in this study. These differences in sodium concentrations among sites may be explained by the reduction in sodium availability in areas located further inland compared to areas close to the ocean (Kaspari et al. 2008). For *Piper* species data are limited. A single study by Studier et al. (1995) reports an average sodium concentration of 730 ± 60 ppm for species of *Piper* from northeastern Peru, which is substantially higher than our findings. This difference between northeastern and southeastern Peru may be due to historical processes such as the mid-Miocene marine incursion through the Maracaibo Basin in northern South America (Hoorn 1993; Vonhof et al. 1998). This incursion could have increased the sodium availability in the soils where Studier et al. (1995) collected the samples. Thus, based on the results of our study and others conducted in the same region (i.e., Brightsmith et al. 2008; Gilardi 1996), we conclude that sodium in southeastern Peru is more limited for vertebrate folivores and frugivores than in other regions.

Ficus and *Piper* species contain sufficient concentrations of magnesium and potassium for bats. Average concentrations of magnesium for both genera (2,580 ppm for *Ficus* and 2,560 ppm for *Piper*) surpassed the demands for maintenance and reproduction estimated for small mammals (500 and 600–700 ppm, respectively—National Research Council 1995). Frugivorous bats can thus meet their magnesium demands from their diets. Although there were differences in the concentrations of potassium between *Ficus* and *Piper* fruits, both genera contained enough to meet the maintenance and reproductive requirements estimated for small mammals (2,000–3,600 ppm—National Research Council 1995). The concentrations found in this study are similar to those of other localities in the tropics (Gilardi 1996; Nagy and Milton 1979; O'Brien et al. 1998; Wendeln et al. 2000).

Sodium-limitation hypothesis and bat's lick visitation.—*Ficus* chemistry supports the sodium-limitation hypothesis for lick visitation by stenodermatine bats, one of the most speciose Neotropical bat assemblages (Gardner 2008). Sodium, an essential element for osmoregulation, nerve impulses, and muscular function in vertebrates (Michell 1995), is found in significantly lower concentrations in *Ficus* fruits in the southeastern Peruvian Amazon compared to other geographical regions (Nagy and Milton 1979; O'Brien et al. 1998; Wendeln et al. 2000). Consequently, bats or other animals feeding primarily on fig fruits, or other plants and plant parts with low sodium content, may potentially face sodium constraints unless they supplement their diets with high-sodium sources such as licks. The daily minimal requirements of sodium estimated for small mammals (500 ppm [National Research Council 1995]; which increases during reproduction [Michell 1995]) exceed by 30-fold the concentrations in the *Ficus* fruits analyzed in the present study. For stenodermatine bats, the daily requirement for an adult *Artibeus jamaicensis* is 14 mg sodium animal^{-1} day^{-1} (Studier and Wilson 1991). If *A. jamaicensis* feeds exclusively on *Ficus* with 1,690 ppm of sodium (as in Central America [Wendeln et al. 2000]), bats would need to ingest approximately 10 fruits per day to meet the minimal sodium requirements. In southeastern Peru, a frugivorous bat would need to ingest more than 100 *Ficus* fruits per day. Because flying to search for fruits demands high levels of energy (Korine et al. 2004; Speakman 2008), it is possible that bats choose less costly mechanisms to supplement their low-sodium fruit diets, such as the use of natural licks, especially during reproduction. Furthermore, high concentrations of potassium in plant tissue can decrease the assimilation of sodium (Weeks and Kirkpatrick 1976), thus sodium deficiency in bats would not be ameliorated only by increasing the consumption of potassium-rich plants.

The complementary results observed in this study among patterns of lick visitation by stenodermatine bats, their specialized *Ficus* diet, and the low sodium content in *Ficus* fruits, with the consistently high concentration of sodium in lick water reported by Bravo et al. (2010a, 2010b) strongly support the sodium-limitation hypothesis as an explanation for lick visitation by stenodermatine frugivorous bats in the southeastern Peruvian Amazon. An alternative explanation for lick visitation by bats is that clay renders dietary toxins less harmful for stenodermatine bats (Voigt et al. 2008). However, because ripe *Ficus* fruits contain low concentrations of secondary compounds (Janzen 1979; Wendeln et al. 2000), this hypothesis does not seem to be the main explanation for lick visitation by *Ficus*-specialist bats.

Because *Piper* species also had low concentrations of sodium, carolliine bats feeding exclusively on *Piper* could potentially face sodium limitation. However, as in other studies, we found that carolliines supplement their diets with insects. Although we were not able to identify insects found in fecal samples, York and Billings (2009) report a variety of insects in the diets of 6 *Carollia* species. If these insects had significantly higher concentrations of sodium compared to *Piper* fruits (as found by Studier et al. [1994]—540 ppm for 181 lepidopteran species and 1,660 ppm for 43 coleopteran species from a temperate forest), we could suggest that insects may function as supplementary sources of sodium for carolliine bats. However, data are limited on insect sodium content for the Neotropics. So, further investigation into the mineral content of insects consumed by carolliines is required to completely understand sodium intake in carolliines.

The results of our study are consistent with studies conducted on parrot geophagy in the same region of Peru. Parrots consume sodium-rich soils from licks (Brightsmith and Aramburú 2004; Brightsmith et al. 2008; Emmons and Stark 1979; Powell et al. 2009) and plants consumed by parrots have low concentrations of sodium compared to plants from other regions (Brightsmith et al. 2008; Gilardi 1996). In addition, whereas the presence and use of licks by parrots in South America is concentrated in regions where sodium is relatively scarce, licks are absent in nutrient-poor regions, such as the Guianan and Brazilian shields, where it is predicted that plants would have high concentrations of toxins for defense (Lee et al. 2010). Thus, although clay consumption at licks also may provide protection from plant dietary toxins (Gilardi et al. 1999), Lee et al. (2010) suggested sodium limitation is the most-parsimonious explanation for parrot geophagy, similar to our study.

Although there is still no clear evidence to suggest that licks may have an effect on animal biodiversity at large scales, the geographic limitation of sodium in fruits, especially *Ficus*, could have certain implications on local community structure. *Ficus* is considered a keystone species in the tropics and is consumed by a great variety of organisms (Janzen 1979; O'Brien et al. 1998; Terborgh 1986). In areas such as southeastern Peru, where *Ficus* fruits have low sodium concentrations, *Ficus*-specialist bats would not be able to survive on a diet with such low sodium concentrations. Thus, bat communities would potentially be impoverished if mineral licks were not present. Comparative studies of frugivorous bat assemblages, as well as detailed patterns of sodium content in *Ficus* and access to natural licks across sites at a continental scales, could provide insights into the mechanisms maintaining tropical bat diversity. In addition, our results suggest an important mechanistic link between frugivorous bats and terrestrial ecosystem engineers (e.g., geophagous tapirs and peccaries [Beck et al. 2010]) that make soil-borne resources available. Bats drink sodium-rich water that accumulates in soil depressions made by larger geophagous mammals that visit licks, such as tapirs and white-lipped peccaries (Tobler et al.

2009). Accordingly, bats benefit from the mechanical action of these mammals at licks. In addition, the role of bats as important dispersers of *Ficus* (Ascorra et al. 1996; Giannini and Kalko 2004; Kalko et al. 1996) benefits the whole community of *Ficus* consumers, including tapirs and peccaries. However, large ungulates are among preferred prey of hunters (Bodmer 1995), who use licks as hunting sites (A. Bravo, pers. obs.). If ungulates were extirpated from local communities where bats use licks, the availability of sodium sources for bats would be imperiled, which could potentially affect bat communities and processes of seed dispersal. Consequently, the present study not only provides a key piece of evidence to explain lick visitation by bats, but also reveals an intricate net of interrelationships among tropical plants and mammals that may have numerous implications for understanding and preserving tropical rain-forest ecosystems.

RESUMEN

La geofagia es un comportamiento común entre animales que se alimentan de plantas. En los Neotrópicos, los saladeros, llamados también *collpas*, son centros de actividad de los murciélagos frugívoros (Stenodermatinae). Estos murciélagos toman agua con alto contenido de minerales que se acumulan en las depresiones hechas por mamíferos geófagos terrestres. Dos hipótesis mecanísticas han sido propuestas para explicar este comportamiento: los saladeros son fuentes confiables para suplementar nutrientes limitados, especialmente sodio; y los saladeros proveen sustancias que hacen las toxinas de la dieta menos dañinas. Nosotros evaluamos la primera hipótesis a través de un análisis de la dieta de los murciélagos en conjunto con la química de los saladeros en la Amazonía peruana. Encontramos que la mayoría de los murciélagos que visitan los saladeros pertenecen a la subfamilia Stenodermatinae y que son especialistas en *Ficus* – un recurso clave. Además, encontramos que a pesar de que los frutos de *Ficus* en el sureste peruano son buenas fuentes de algunos minerales, sus contenidos de sodio son limitados en relación a los requerimientos fisiológicos de un mamífero pequeño. Por otro lado, murciélagos de la subfamilia Carolliinae complementan sus dietas de frutas con insectos, una fuente potencial de sodio. Los resultados complementarios entre la dieta de los murciélagos, la química de *Ficus*, y la química del agua de los saladeros apoyan fuertemente la hipótesis de la limitación de sodio para explicar el uso de saladeros por murciélagos y además sugieren una relación estrecha entre estos murciélagos y los ingenieros de ecosistemas terrestres que mantienen los saladeros disponibles. Debido a que el sodio es un nutriente esencial para los vertebrados y el *Ficus* es un recurso clave para muchas especies animales, nuestros resultados pueden tener implicancias para la comunidad de vertebrados frugívoros donde el sodio es limitado. Los saladeros podrían jugar un papel crítico como fuentes de sodio y por lo tanto deberían ser consideradas como recursos estratégicos de conservación.

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APPENDIX I

Concentrations in parts per million (ppm) and parts per hundred (%) of 12 elements for fruits of 10 species of *Ficus* and 6 species of *Piper* collected in Los Amigos Conservation Concession in Madre de Dios, southeastern Peru. Replicates for a species represent fruit samples collected from different individuals (trees for *Ficus* and shrubs for *Piper*).

Family and species	Boron (ppm)	Calcium (%)	Copper (ppm)	Iron (ppm)	Magnesium (%)	Manganese (ppm)	Nitrogen (%)	Phosphorus (%)	Potassium (%)	Sodium (ppm)	Sulfur (%)	Zinc (ppm)
Moraceae												
Ficus americana	21.717	0.850	10.225	118.184	0.395	337.711	1.232	0.128	1.006	25.561	0.113	23.266
Ficus americana	23.173	0.679	10.086	78.047	0.412	392.636	1.210	0.127	1.140	38.523	0.110	26.446
Ficus insipida	16.164	1.725	9.050	153.907	0.385	42.245	1.243	0.173	2.148	19.683	0.145	17.646
Ficus insipida	16.780	1.891	8.690	93.383	0.411	61.292	1.267	0.182	2.184	25.912	0.154	18.507
Ficus juruensis	14.662	0.860	9.784	66.680	0.115	13.673	0.764	0.137	1.335	17.365	0.064	19.161
Ficus juruensis	15.949	0.963	9.752	76.762	0.127	15.392	0.819	0.146	1.394	23.558	0.072	20.673
Ficus maxima	25.411	0.889	6.499	85.191	0.233	25.866	1.517	0.175	2.445	42.098	0.138	15.884
Ficus maxima	25.422	0.900	6.679	66.487	0.239	36.234	1.507	0.180	2.437	36.683	0.137	16.707
Ficus sp. 1	18.383	0.793	7.840	47.142	0.191	26.439	1.510	0.195	2.619	15.284	0.136	16.604
Ficus sp. 1	19.056	0.749	7.211	46.444	0.185	25.100	1.482	0.188	2.722	28.666	0.135	16.790
Ficus sp. 2	14.285	0.409	13.734	287.287	0.191	12.903	1.308	0.222	2.102	8.709	0.109	23.664
Ficus sp. 2	14.508	0.438	12.634	149.304	0.188	12.217	1.281	0.224	2.137	5.567	0.110	24.652
Ficus sp. 3	14.901	0.709	6.271	37.407	0.288	177.536	1.028	0.128	2.226	7.301	0.085	8.742
Ficus sp. 4	13.747	0.718	7.587	48.586	0.298	210.872	1.012	0.124	1.978	8.463	0.088	11.519
Ficus sp. 4	13.896	0.779	6.158	31.834	0.277	203.044	0.979	0.111	1.964	1.691	0.080	8.764
Ficus sp. 4	14.137	0.700	5.455	26.041	0.281	186.526	1.067	0.126	2.102	12.870	0.085	9.055
Ficus sp. 4	13.591	0.729	6.249	25.953	0.281	174.985	0.995	0.123	1.986	12.877	0.084	8.545
Ficus sp. 5	16.413	0.236	10.744	33.829	0.203	144.345	1.091	0.111	1.656	18.353	0.069	14.891
Ficus sp. 5	15.232	0.244	10.355	35.950	0.204	145.604	1.104	0.110	1.598	13.519	0.068	15.402
Ficus sp. 6	10.897	0.819	17.222	50.558	0.256	54.747	1.411	0.149	1.285	9.075	0.102	24.332
Ficus sp. 6	11.410	0.745	15.531	49.213	0.264	50.010	1.484	0.173	1.420	4.682	0.096	22.255
Ficus sp. 6	11.765	0.688	15.237	44.591	0.257	58.888	1.128	0.123	1.391	6.299	0.090	21.656
Piperaceae												
Piper augustum	8.901	0.120	20.147	21.091	0.262	127.558	1.719	0.193	2.190	25.531	0.138	14.683
Piper augustum	8.789	0.108	22.263	14.992	0.206	90.491	1.528	0.166	2.113	14.283	0.109	15.112
Piper augustum	8.945	0.097	22.093	13.462	0.170	127.651	1.425	0.155	2.095	14.729	0.109	15.122
Piper augustum	7.353	0.137	17.463	23.433	0.177	106.567	1.804	0.196	1.424	8.915	0.112	11.095
Piper sp. 1	9.036	0.157	17.153	42.831	0.440	644.968	1.667	0.198	1.697	12.780	0.142	11.532
Piper sp. 1	9.099	0.160	16.046	38.722	0.420	616.166	1.573	0.179	1.720	6.371	0.133	11.388
Piper sp. 2	26.208	0.630	18.962	38.214	0.202	64.571	2.187	0.212	1.440	55.289	0.141	27.495
Piper sp. 2	13.329	0.568	14.071	54.225	0.230	208.589	1.890	0.199	1.100	36.711	0.142	32.397
Piper sp. 3	21.524	0.393	19.487	38.190	0.307	918.752	2.759	0.237	1.544	39.432	0.189	51.857
Piper sp. 4	14.563	0.372	28.570	83.615	0.248	639.523	1.664	0.194	1.387	23.138	0.137	34.101
Piper sp. 5	9.370	0.251	10.233	20.307	0.210	29.435	1.368	0.278	1.489	6.769	0.155	12.871
Piper sp. 5	8.716	0.243	10.388	20.675	0.197	21.854	1.502	0.244	1.450	3.596	0.152	12.525

APPENDIX II

Number of captures of bat species of the subfamilies Carolliinae and Stenodermatinae (Phyllostomidae) at lick, forest, and gap sites in the Peruvian Amazon. Number of captures in bold indicates bat species overrepresented at the site. An asterisk (*) indicates $P < 0.001$ from comparisons among licks versus forest versus gap sites. Bat nomenclature follows Gardner (2008).

Subfamily and species	Lick	Forest	Gap	*G*-value
Carolliinae				
Carollia brevicauda	3	**18**	**29**	24.6*
Carollia perspicillata	7	**40**	**26**	25.76*
Rhinophylla pumilio		**24**	**10**	33.51*
Stenodermatinae				
Artibeus lituratus	**208**	26	21	251.95*
Artibeus obscurus	**210**	40	18	237.04*
Artibeus planirostris	**318**	36	11	470.49*
Chiroderma salvini	**54**			118.65*
Chiroderma trinitatum	**146**	2		304*
Chiroderma villosum	**64**	1		132.49*
Platyrrhinus brachycephalus	**72**	3		139.6*
Platyrrhinus helleri	**238**	4	1	480.19*
Platyrrhinus infuscus	**58**	4	3	88.84*
Sphaeronycteris toxophyllum	**18**			39.55*
Sturnira lilium	**29**		5	118.65*
Uroderma bilobatum	**265**	2	3	536.72*
Uroderma magnirostrum	**89**	8	2	142.71*
Vampyriscus bidens	**89**		1	186.8*
Vampyriscus pusilla	**27**			24.6*
Vampyrodes caraccioli	**21**			46.14*

APPENDIX III

Loading values for the first 2 principal components (PC1 and PC2) from the principal component analysis of the mineral content of *Piper* and *Ficus* fruits.

Mineral	PC1	PC2
Boron	−0.116	−0.540
Calcium	0.117	−0.504
Copper	−0.319	0.353
Iron	−0.014	−0.287
Magnesium	−0.099	−0.136
Manganese	−0.309	0.117
Nitrogen	−0.476	0.060
Phosphorus	−0.334	0.072
Potassium	0.126	−0.190
Sodium	−0.291	−0.378
Sulfur	−0.415	−0.101
Zinc	−0.394	−0.131

APPENDIX IV

Diet composition of bats (Phyllostomidae) captured at licks in the southeastern Peruvian Amazon. Numbers of fecal samples containing each constituent are presented. Abbreviations are as follows: Araceae (Ara.), Clusiaceae (Clu.), and undetermined (Und.). Bat nomenclature follows Gardner (2008).

	Seeds							
	Moraceae		Piperaceae					
Subfamily and species	*Cecropia*	*Ficus*	*Piper*	Ara./Clu.	Pulp	Soil	Insects	Und.
Carolliinae								
Carollia brevicauda								2
Carollia perspicillata			3	1				
Stenodermatinae								
Artibeus lituratus	9	2						
Artibeus obscurus	4	12			1			
Artibeus planirostris	1	12			1	2		
Chiroderma salvini		3						1
Chiroderma trinitatum		2				2		
Chiroderma villosum		3			1	1		
Platyrrhinus brachycephalus	4	1						
Platyrrhinus helleri	1	1			1			
Platyrrhinus infuscus	8	4				2		
Sturnira lilium	1		2	1				1
Uroderma bilobatum		8			2	1		
Vampyriscus bidens		1						
Vampyriscus pusilla		1						
Total	28	50	5	2	6	8	0	4

APPENDIX V

Diet composition of bats (Phyllostomidae) captured in forest sites in the southeastern Peruvian Amazon. Numbers of fecal samples containing each constituent are presented. Abbreviations are as follows: Araceae (Ara.), Clusiaceae (Clu.), Cucurbitaceae (Cuc.), Solanaceae (Sol.), and undetermined (Und.). Bat nomenclature follows Gardner (2008).

	Seeds							
	Moraceae		Piperaceae					
Subfamily and species	*Cecropia*	*Ficus*	*Piper*	Ara./Clu./Cuc./Sol.	Pulp	Soil	Insects	Und.
Phyllostominae								
Phylloderma stenops				1				
Phyllostomus elongatus	2						3	
Phyllostomus hastatus	4							
Carolliinae								
Carollia brevicauda	3		6	1	1			
Carollia perspicillata	1		8	1	3		3	1
Rhinophylla pumilio			1	6	2		1	
Stenodermatinae								
Artibeus obscurus	1	2	1					
Artibeus planirostris	2	1						
Chiroderma trinitatum		1						
Mesophylla macconnelli					1			
Platyrrhinus infuscus	1							
Sturnira lilium				2				
Total	14	4	16	11	7	0	7	1

APPENDIX VI

Diet composition of bats captured in gaps in the southeastern Peruvian Amazon. Numbers of fecal samples containing each constituent are presented. Abbreviations are as follows: Araceae (Ara.), Clusiaceae (Clu.), Solanaceae (Sol.), and undetermined (Und.). Bat nomenclature follows Gardner (2008).

	Seeds							
	Moraceae		Piperaceae					
Family, subfamily, and species	*Cecropia*	*Ficus*	*Piper*	Ara./Clu./Sol.	Pulp	Soil	Insects	Und.
Phyllostomidae								
Phyllostominae								
Phyllostomus elongatus	1		1		1		1	
Phyllostomus hastatus	2							
Carolliinae								
Carollia benkeithi			6	1	1		1	2
Carollia brevicauda	2		12	1	3		1	2
Carollia perspicillata	3		19	3			4	4
Rhinophylla pumilio	2		2	1			2	
Stenodermatinae								
Artibeus obscurus	1							
Mesophylla macconnelli					1			
Sturnira lilium		1						
Thyropteridae								
Thyroptera tricolor							1	
Total	11	1	40	6	6	0	10	8